COMPARITIVE DIET AND HABITAT SELECTION OF PUKU (*KOBUS VARDONII*) AND LECHWE (*KOBUS LECHE*) ON THE CHOBE RIVER FLOODPLAIN, BOTSWANA.

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A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfillment of the requirements for the degree of Master of Science.

Orlando, Florida, USA, 2010

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

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___19th_ day of ____October_____2010

Abstract

The influence of ecological change on the populations of select herbivores is of concern to national parks and wildlife managers in many regions of the world. Impacts of burgeoning elephant (*Loxodonta africana*) populations recovering from early 20th century hunting pressure have been well documented. Puku (*Kobus vardonii*) antelope within the Chobe National Park, Botswana, are believed to be at risk of local extinction due to ecological change resulting from an increasing elephant population. In this study, I sought to compare the low density puku population to the high density, congeneric lechwe (*Kobus leche*) population that inhabits the floodplains adjoining the Chobe River. With this project I aimed to improve our understanding of forage selection, nutritional status, and habitat selection of puku in relation to the more regionally distributed, high density lechwe. Theories of feeding specialization, competition, and patterns of species abundance suggested that the low density puku would be more selective in forage and habitat resources as well as being more constrained nutritionally than the high density lechwe. My results showed puku to feed on a wider range of grass species than lechwe, but to be more narrowly selective of grasses in terms of phenotypic features. Puku were more narrowly selective of grass greenness, height, and cover than were lechwe. Puku and lechwe shared high levels of dietary overlap across seasons, only differing in contributions of a few key grass species. There was no distinction between puku and lechwe nutritionally with both species appearing to remain above critical thresholds for faecal nitrogen and phosphorus. The two grazers show slight partitioning of habitat use during the low water season. During the high water season, puku and lechwe showed near complete partitioning of habitat use by implementing differing strategies of selection in response to the inundation of the floodplains. Overall, results showed slight partitioning of food resources, but more definitive differentiation in habitat use between puku and lechwe. My findings suggest that due to the close similarities in diet, nutrition, and habitat selection between the low density puku and high density

lechwe, some other factor, such as predation, may be limiting the population density of puku within the Chobe National Park.

For my family,

New and old,

19th October, 2010.

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CHAPTER 1

INTRODUCTION TO THE STUDY

1.1 The context of the study

Over the past 150 years, the Chobe riverfront in northern Botswana has experienced profound ecological changes. A temporary reduction in the numbers of large herbivores due to hunting and the rinderpest panzootic led to the establishment of woodlands along much of the riverfront (Simpson, 1978). From the mid 1900s, herbivore populations began to recover and in particular, the rapid increase in the elephant (*Loxodonta africana*) population beginning in the 1960s led to a decline in woody vegetation along the riverfront (Child, 1968; Campbell, 1990; Mosugelo *et al.,* 2002; Rutina *et al.,* 2004). Floodplain vegetation is also reported to have changed with dominant grass species today not mentioned among common species found by Simpson (1978) in 1969/70.

In light of the abovementioned habitat changes, the Botswana Department of Wildlife and National Parks (DWNP) are concerned that the puku population may have declined since the last census conducted by Child (1968) and Child & von Richter (1969) in 1965 – 1967. The distribution of puku (*Kobus vardonii*) in Botswana is highly localized and restricted to a 25 km stretch of floodplains along the Chobe River within the Chobe National Park. A study conducted by Dipotso & Skarpe (2006) in 2001 – 2003 indicated that the puku population had increased in numbers since the 1960s but the concentration of the population had shifted eastwards, possibly as a result of direct human disturbance along the western part of the riverfront. New concern within the DWNP is that due to this eastward population shift and associated habitat constriction, puku antelope, already considered vulnerable in southern Africa, may be at risk of local extinction in the Chobe National Park.

Ross *et al.* (1998) estimated that this relict population persists in numbers of less than 100 individuals; however, Dipotso & Skarpe (2006) in their study from 2001 to 2003 estimated the population to be approximately 127 animals (*95% C.I.* 108.7 – 143.3). Since this is the only puku population in Botswana, a population estimate of 127 animals, places the puku population firmly at risk of local extinction.

Although concerns have been raised about the status of puku antelope in Botswana, considerably less concern is shown towards the closely related red lechwe (*Kobus leche*). Southern African lechwe populations along the Chobe River front, further west along the Kwando/Linyanti/Chobe river system, and within the Okavango Delta are reported to number within tens of thousands (East, 1989**;** Mills & Hes, 1997).

Lechwe and puku are considered to be floodplain species (Allen, 1963; Child & Von Richter, 1969; Lent, 1969; Bell, 1970) whose movements are strongly influenced by changes in water levels (Williamson, 1990). Lechwe and puku reportedly occupy similar habitats and consume similar diets (Child & Von Richter, 1969; Rees, 1978; Williamson, 1990; Dipotso & Skarpe, 2006), and it is this point that was of particular interest to the study. If these congeneric species are documented as consuming similar diets and utilizing similar habitats, what factors enable lechwe to exist along the western and eastern stretches of the Chobe riverfront, and what factors are limiting the distribution of puku to the eastern reaches? By defining specific differences in diet and habitat use between these two congeneric species, we will improve our understanding of the specific niche occupied by puku within the Chobe National Park. The outcomes of this study will contribute towards a better understanding of the ecology of a rare and vulnerable antelope and aid the Botswana Department of Wildlife and National Parks in future policy making and conservation of the species.

1.2 Taxonomy and distribution

The genus *Kobus* is recognized as containing five species; waterbuck, *Kobus ellipsiprymnus* (Ogilby, 1833); lechwe, *Kobus leche* (Gray, 1850); Nile lechwe, *Kobus megaceros* (Fitzinger, 1855); puku, *Kobus vardonii* (Livingstone, 1857); and Kob, *Kobus kob* (Erxleben, 1777). The genus is widely distributed throughout Africa extending from Senegal on the western coast to Ethiopia and Somalia in the east (Kingdon, 1997). The northern reaches of the distribution extend into Eritrea and the Sudan while the northern provinces of South Africa mark the extreme southern extent of the *Kobus* genus (Kingdon, 1997).

Three species of the genus occur in the Southern African sub-region (Southern Africa is defined as encompassing Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland, and Zimbabwe) namely, puku, lechwe and waterbuck. Within Southern Africa puku and lechwe are highly localized in their distribution. Puku are restricted to the eastern reaches of the Chobe River within the Chobe National Park in northern Botswana. The puku found on the floodplains of the Chobe River are the southernmost population of the species which has its center of distribution in Zambia and southern Democratic Republic of Congo (Mills & Hes, 1997; **Figure 1**).

In Southern Africa lechwe have a slightly wider distribution than puku which includes the Chobe, Linyanti, Kwando and Okavango River systems in northern Botswana. The Okavango Swamps mark the southernmost population of the species which has its center of distribution along the borders of south-eastern Angola and south-western Zambia (Kingdon, 1997; **Figure 2**).

1.3 General characteristics

The puku is a medium sized antelope with males reaching a mean body weight of 77kg and a mean shoulder height of 0.92m and females with a mean body weight of

61kg and a mean shoulder height of 0.84m (Mills & Hes, 1997). Puku have longish coarse coats that are generally golden brown in colour. The underside of the body is slightly paler in colour with conspicuous white rings around the eyes. Only the males have horns. The horns are lyre-shaped, strongly ridged and do not exceed 55cm in length.

Lechwe are slightly larger than puku. Males reach an average body weight of 118kg and a mean shoulder height of 1m, whereas females average 74kg in body weight and around 0.90m at the shoulder (Mills & Hes, 1997). Similar to puku, lechwe have a longish coarse coat but the colour is a bright chestnut brown. The underpart, neck and chin are noticeably white and the fronts of the forelegs have a black stripe. Again, only the males have horns. The horns are back-slanting with upturned tips and may reach a length of 92cm.

1.4 Ecology and behaviour

As with typical antelope behaviour, puku and lechwe have peak feeding and activity periods during the early morning (07h00 – 10h00) and late afternoon (15h00 – 18h00) (R. O'Shaughnessy, Personal Observation). Typical habitats for both species include river floodplains and nutrient rich grasslands (Spinage, 1986). Lechwe however, are extremely at ease in water and are commonly sighted feeding in shallow swamp areas.

Both puku and lechwe are highly dependent on water. During the rainy season, and in times of flood, puku will move to upland areas and will often inhabit woodland areas adjacent to inundated floodplains (Alden *et al.,* 1995; Kingdon, 1997). During seasonal floods lechwe move in synchrony with the rise of the water and will feed on the periphery of the floodplain (Walther, 1990; Alden *et al.,* 1995; Kingdon, 1997).

Lechwe population densities may be extremely high, often exceeding 200 individuals per square kilometer. Male lechwe typically exhibit 'lekking'. Within a lek, a number of males will defend small patches of clustered territories within a common arena (Walther, 1990, Nowak, 1991, Alden *et al.,* 1995). Herds of female lechwe will move independently of these clustered male territories, except during oestrus when herds of females may be associated with the territory of a particular male.

Puku occur in densities lower than those of lechwe. During the dry season groups of 50 or more puku may be observed along the margins of watercourses. Solitary males defend territories throughout the year. Herds of females pass through these territories and each male attempt to induce the females to stay within his patch for as long as possible (Wilson & Reeder, 1993; Alden *et al.,* 1995; Kingdon, 1997).

1.5 Habitat selection

Animals do not use the landscape in a random fashion, and variation in habitat choice and food preferences will give an uneven utilization of the vegetation both on landscape and local scales. Mduma & Sinclair (1994) propose three hypotheses explaining habitat selection in antelope: **1)** habitats are chosen to minimize the cost and maximize the benefits of obtaining resources, **2)** habitat selection results from niche partitioning due to competition for resources, **3)** habitat selection functions to reduce predation by using escape terrain and by associating with other species for mutual protection.

Grazers will typically favour newly emerging shoots and this will result in patchy grazing effects on the landscape as the phenology of plants interacts with nutritional needs and behaviour of the animal. Because forage in grasslands is generally of low quality and spatio-temporally variable, where herbivores choose to feed and which plant species they select to graze will have a significant impact on whether or not dietary requirements are met (Frank, 2008). Furthermore, forage in grassland is

heterogeneous at many different scales and herbivores must make a series of important hierarchically organized feeding decisions that include: which range to move to seasonally; which portions of a landscape to graze each day; and which plant or plant part to bite (Senft *et al.,* 1987).

The quality and quantity of resources available to herbivores vary considerably both spatially and temporally throughout the seasonal climatic cycle. Coupled to the climatically induced cycles of resources, additional factors such as predation and competition may affect the accessibility of forage to herbivores. In response to these fluctuations and restrictions in forage quality and quantity, herbivores have evolved a range of foraging strategies to maintain nutrient intake (Owen-Smith, 2005). Spatially, herbivores seek to feed in patches providing resources that contain adequate digestible nutrients which support growth and reproduction. Temporally, herbivores may adjust foraging behaviour and/or exploit key resource areas in response to variation in resource quantity and quality (Owen-Smith, 2005; Knoop & Owen-Smith, 2006).

As outlined by O'Reagain (2001), spatial variability can be addressed using a plant based approach beginning at the plant part and extending upwards to the plant, patch, landscape and regional scale. The finest level of spatial heterogeneity encountered by an herbivore is distinguishing between plant parts. This scale of heterogeneity may vary from a few millimeters to a few meters depending on the phenology and size of the plant. Variability at the level of the plant part arises due to differences in nutritional quality between the plant organs and the various levels of maturity of the plant parts. Green leaf is the highest quality component in a grass sward and has significantly higher quality than either stem or dead material (Wilson, 1981). Grazing animals prefer green leaf material to dry, stemmy or dead plant parts, because the proportion of green leaf in the diet is positively correlated with diet quality (Chacon & Stobbs, 1976; Grobler, 1981; Winkler, 1992; O'Reagain, 2001).

During the dry season and critical periods when no plant growth occurs, grazers are able to maintain the levels of greenness in their diet by expanding the diet breath over a range of green leaf availabilities. Grazers select the most accessible bites within grass swards, but the extent to which this is possible depends on trade-offs between bite size and bite quality. A grazer will be constrained by the size of its mouth, and thus the amount of forage that may be immediately ingested will depend largely on the height of the grass sward. Grazers therefore select species based on the balance between nutrient content and the energetic costs of harvesting and processing a particular grass species (O'Reagain, 2001).

Habitats consist of a mosaic of plant species each varying in quality, height, leaf density and accessibility. Apart from inter-species variation, intra-species variation may occur due to localized differences in soil characteristics, hydrology and defoliation history (Gammon & Roberts, 1978). Grazers typically accept grass species based on interplay between leaf quality and the rate at which leaf material can be harvested (Illius *et al.,* 1999). While grazing on floodplains, kob (Fryxell & Sinclair, 1988; Klop & Van Goethem, 2008) and lechwe (Williamson, 1990) are known to select short, non-stemmy grass species with leaves of high quality and low tensile strength and avoid species that are tall and stemmy with tough leaves of low quality.

Food items available to herbivores may be concentrated in patches constituted by a tree, shrub or extended herbaceous sward (Owen-Smith, 2002). To a large extent patches are generated by the feeding responses of herbivores to particular forms of heterogeneity in the vegetation (Owen-Smith, 2002). At a single site, patchiness could therefore occur simultaneously at multiple overlapping scales. Herbivores respond to patchiness in the environment by avoiding low quality, unproductive patches and concentrating in high quality, productive patches. Feeding within patches of higher quality reduces foraging time, and agrees with optimal foraging

theory, as the animal is able to meet its energetic requirements by digesting lower quantities of food.

Landscapes are composed of landscape units, defined as areas that differ markedly in species composition, vegetation structure, location of nutrients and location of water (O'Reagain, 2001). Existing studies suggest a species may select its habitat at the landscape level based primarily on the key limiting factor of that animal i.e. if predation is the primary limiting factor of the animal, then animals would first select landscapes with lower predation risk with forage quality and quantity being important at smaller spatial scales. Alternatively, forage quality and quantity may be the primary limiting factor of the animal at the landscape level, with predation risk being secondly important at finer spatial scales (Rettie & Messier, 2000).

Regions are defined by major differences in climate, geology, soils and vegetation (O'Reagain, 2001). In animal terms, regions are equivalent in scale to migratory ranges (Senft *et al.,* 1987). The response of animals to regional and landscape heterogeneity is similar, and selection tends to be based on factors such as forage quality and quantity, predation risk and proximity to water.

1.6 Feeding ecology

Relatively few studies have been conducted documenting the diet of puku and lechwe. However, puku and lechwe may be considered to be ruminants preferring fresh grass and with a high dependence on water. In the Chobe National Park, Child & Von Richter (1969) record both puku and lechwe as being exclusively grazers. Mills & Hes (1997) reaffirm the findings of Child & Von Richter but add that at times puku are known to accept highly nutritious forage of dicotyledons such as *Cassia spp.* and *Kigelia africana*. Also, within the Linyanti Swamps, Williamson (1990) identified sedges (25%) and dicotyledons (21%) to form a sizable portion of the diet of lechwe – the remainder of the diet being composed of grasses.

Due to the animal populations and habitat changes in the Chobe River region (Child, 1968; Simpson, 1978; Campbell, 1990; Mosugelo *et al.,* 2002; Rutina *et al.,* 2004; Dipotso & Skarpe, 2006), it is likely that the composition of the grasses in the diet of both lechwe and puku may have changed in the 38 years since the study of Child & Von Richter (1969). At present the floodplains of the Chobe River are dominated by *Cynodon dactylon* and *Vetiveria nigritana* (Dipotso & Skarpe, 2006). *C. dactylon* is a short, mat forming grass that grows well under conditions of high grazing. *V. nigritana* is a tall grass that grows in dense tufts. Both species have a high grazing value under normal conditions and it is therefore expected that due to the dominance of these species on the floodplain puku and lechwe are likely to consume both grasses in their diet.

In terms of nutrient composition, the most significant and critical variation in resource quality and quantity is the result of temporal variability occurring at the scale of months to years. Temporal variability at this scale arises due to coupling of plant growth cycles with seasonal changes in rainfall, soil moisture and temperature. During favourable months, such as the wet season, grazed resources are able to regrow quickly and thus, even heavy grazing has no lasting effect on the ecosystem. During the unfavourable dry season, regrowth of grazed resources ceases and animals may begin to utilize a wider range of spatial scales by utilizing species, patches or landscape units that were previously avoided or only lightly grazed. By the end of the dry season, previously avoided resources may also become depleted and animals are faced with a critical period in nutrition. Owen-Smith (2005) proposed a generic set of resource types to elucidate the relative importance of different food types through the seasonal cycle for browsing and grazing animals:

- **Quality resources** are high quality foods/areas that provide high intake rates but generally have restricted accessibility.
- **Staple resources** supply adequate levels of nutrition and provide the bulk of the diet for most of the season.

- **Key resources** are those resources of generally low quality and are less favoured by the animal but can sustain maintenance levels in times of need; key resources are those that buffer animals through critical periods.

Critical periods for floodplain ruminants, such as puku and lechwe, may occur during periods that are normally expected to be favourable to herbivores. Inundation of floodplains during the wet season may drive puku and lechwe into adjoining upland areas that are avoided during other periods. Quality and stable resources may no longer be accessible or available leaving only key resources for sustenance.

1.7 Nutritional status

Attempting to determine the nutritional status of animals through forage quality estimates may not be accurate due to selection of forage by individual animals (Cook *et al.,* 1994). Other methods used in the determination of nutritional status such as fistulation and slaughtering are not only expensive, but unethical. Faecal analyses may provide an alternative by relating chemical characteristics of faeces to the quality of ingested diets (Holechek *et al.,* 1982). Positive relationships mentioned by Holechek *et al.* (1982), Gates & Hudson (1981), Arnold & Dudzinski (1963) and Leslie & Starkey (1985) permit the use of chemical composition of faeces as an index of forage quality (Wrench *et al.,* 1997). Faecal nutrient levels have been used to predict dietary nutrient levels in black-tailed deer (*Odocoileus hemionus columbianus*; Leslie & Starkey, 1985), white-tailed deer (*Odocoileus virginianus*; Jenks *et al.,* 1989), duiker (*Cephalophus monticla*), eland (*Taurotragus oryx*), hartebeest (*Alcelaphus bucelaphus*) and Thomson's gazelle (*Gazella thomsonii*; Robbins, 1983).

Nutritional value of the diet of grazers may be assessed from faecal samples in terms of crude protein, CP_d (Sinclair, 1970). Estimates of crude protein in the diet are

calculated from levels of crude protein found in the faeces, CP_f (Lancaster, 1949 in Duncan, 1975). Levels of CP_f are derived from percentage nitrogen in the faeces since nitrogen is an essential part of biologically important molecules such as proteins and nucleic acids (Solomon, Berg, & Martin, 1999). Nitrogen is considered one of the most limiting nutrients for herbivores (Sinclair, 1977; Berry & Louw, 1982; Ketelaars, 1986).

Where phosphorus deficiency occurs, growth and reproduction are hampered in large herbivores (Grassman & Hellgren, 1993). It has been shown that faecal phosphorus correlates with phosphorus intake (Moir, 1960**;** Belonje, 1980). According to Grant *et al.* (1995) faecal nitrogen and faecal phosphorus should be used in conjunction when predicting nutritional status because their removal from the body in the faeces is linked. The findings of Wrench *et al.* (1997) indicate prediction of dietary phosphorus from faecal phosphorus is robust and one prediction may be used for all species and situations through the use of a combined linear regression model. The prediction of dietary nitrogen in browsers is not as robust as that for dietary phosphorus as it is influenced by the intake of phenolic compounds (Wrench *et al.,* 1997). However, the calibration for grazers is better and thus predictions may be used to determine nitrogen deficiency.

Results from a study by Wrench *et al.* (1997), performed on impala, blue wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli)*, point to values <14g/kg dry mass (DM) to indicate CP_f deficiency and <2g/kg DM to indicate phosphorus deficiency. Rees (1978) found the mean CP_f value to be 16g/kg DM and the mean faecal phosphorus value to be 2.5g/kg DM for lechwe in the Lochinvar NP, Zambia.

1.8 The study area

The Chobe National Park covers an area of roughly 11,700 km^2 in northeastern Botswana with the northern boundary marked by the Chobe River. The Chobe River

forms the international boundary between Namibia to the north and Botswana to the south. The general study area was located along a 35 km stretch of river frontage from Sedudu Island in the east to Ihaha Campsite in the west (**Figure 3)**.

The mean annual rainfall, recorded in Kasane on the eastern edge of the study area, is 685 mm of which approximately 95% falls during the summer months from October to April (**Figure 4**, Department of Meteorological Services Botswana). The mean daily maximum temperature during summer is 32˚C, with a mean of 27˚C in winter (**Figure 5**, Department of Meteorological Services Botswana).

River levels fluctuate widely throughout the year. With the onset of the floods, river levels begin to rise rapidly for 4 months from a low water mark of around 2.2 m at the end of November, reaching a peak of about 5.4 m during March. The river levels then gradually decline over the next 8 months until the low water mark is reached again at the end of November (**Figure 4**, Ministry of Mineral Energy and Water Resources, Botswana). Annually, the area experiences two clearly differentiable seasons which are defined based on the level and timing of the flood and the onset of the rains. The seasons were thus defined as the low water season (LWS), lasting from beginning September to end February, and a high water season (HWS), lasting from beginning March to end August (see **Figure 4** for reference).

Topographically, the general study area consisted of floodplain grasslands to the north on the Botswana side and the Kalahari sand ridge along the escarpment, to the south (**Figure 6)**. The floodplain grasslands are limited in extent by the annual flood and cover the area between the Chobe River and the Kalahari sand ridge (Simpson, 1975). The floodplains are composed of drainage channels and ridges that experience inundation to varying degrees as the flood waters rise and fall. Small depressions within the floodplains may hold water late into the dry season attracting animals such as elephant, hippo (*Hippopotamus amphibious*) and buffalo (*Syncerus caffer*) which

drink and feed on the aquatic vegetation (**Figure 7**). *Cynodon dactylon* and *Vetivera nigritana* dominate the floodplains with species such as *Phragmites mauritianus, Papspalum scrobiculatum, Digitaria eriantha, Brachiaria spp.* and *Eragrostis spp.* being locally dominant in places.

The Kalahari sand ridge shows considerable variation in vegetative species composition. The riparian fringe is dominated by tree species including *Acacia albidia, Faidherbia albida, Garcinia livingstonei, Combretum imberbe* and *Diospiros mespiliformis* (Simpson, 1975). However, in the last 35 years since the study by Simpson (1975) there has been a drastic decline in the density and numbers of *Faidherba albidia* and *Garcinia livingstonei* along the riparian fringe (Skarpe *et al.,* 2004).

Leading up the sand ridge, locally dominant areas of *Croton megalaboris, Combretum mossambicense, Dichrostachys cinera* and *Capparis tomentosa* are common (**Figure 8**). Grass coverage is low in these areas but dominant species include *D. eriantha, Dactylonium giganteum, Panicum deustum, C. dactylon* and *Brachiaria humidicola.* Upon reaching the top of the sand ridge *Baikiaea* woodland dominates. Dominant tree species in the area include *Baikiaea plurijuga, Guibourtia coleosperma* and *Pterocarpus angolensis* (Simpson, 1975), with grass species being much the same as on the sand ridge.

The general study area was divided into five intensive study sites based on the locations of puku and lechwe. Each intensive study area extended northwards from the 'top road', along the crest of the sand ridge, to the main Chobe River channel (**Figure 6**). Sedudu Island, is like the name suggests, an island, in between two branches of the Chobe River. The island is completely devoid of trees, and large herbivores that commonly inhabit the island include hippo, buffalo, elephant, and lechwe. Predominant grass species on Sedudu include; *Phragmites mauritianus,*

Vetivera nigritana, and *Cynodon dactylon.* The island is subject to near complete inundation during the high water periods.

To the north, Watercart comprises a narrow band of floodplain about four hundred meters wide. The floodplain is dominated by *C. dactylon* and *V. nigritana* grass species, and has many drainage channels running roughly parallel to the main river. These channels quickly fill with water during the rains, and hold water long into the dry season. The floodplains become completely inundated during the annual flood. To the south of Watercart comprises the Kalahari Sand Ridge. Along the escarpment within the Watercart study site the dominant vegetation types include; *Combretum spp., B. plurijuga, B. eruciformis,* and *Dactylonium aegyptium.*

Puku Flats and Kabulabula study sites are similar. Both include a narrow band (about 20 m) of *B. plurijuga* along a portion of the western river bank. Grass species composition in these study sites is heterogeneous with many species occurring including; *Acroceras macrum, Aristida spp., Brachiaria spp., C. dactylon, Dactylonium spp.* and *Eragrostis spp.* The north-eastern sections of both study sites have deep wide drainage lines that contain permanent supplies of water. These study sites become isolated 'islands' during the floods. Along the southern sections, deep channels fill with flood water thereby restricting access to these areas to elephant, hippo, lechwe, and puku.

Lechwe flats are comprised of wide, open short grass floodplains which extend northwards from the Kalahari Sand Ridge. In some sections there the floodplains on the Botswana side of the Chobe River are up to 1.2 kilometers wide. The overwhelmingly dominant grass species in this site is *C. dactylon.* Zebra, buffalo, lechwe, and warthog (*Phacochoerus aethiopicus*) were seen in this site.

1.9 Aim of the study

The aim of this study was to highlight possible dietary and habitat deficiencies contributing towards the isolated distribution of puku along the Chobe riverfront in northern Botswana.

1.10 Objectives of the study

1.10.1 Determine and compare the seasonal diet of puku and lechwe.

1.10.2 Evaluate the level of dietary overlap between puku and lechwe across seasons.

1.10.3 Determine a value of preference for grass species in the diet of puku and lechwe.

1.10.4 Identify relationships between the structure and phenological condition of plant species in the diet and the animal preferences of these plants.

1.10.5 Categorize grass species as being staple, quality and/or key resources and determine periods during which these resources were consumed

1.10.6 Establish resource selection functions (RSF) of any particular habitat type for puku and lechwe.

1.10.7 Investigate how the RSF changes in relation to the seasons.

1.10.8 Analyse any differences between the RSF of puku and lechwe in each of the seasons.

1.10.9 Determining the effects of vegetative physical characteristics and topographical features on the RSF.

1.10.10 Estimating and comparing the used population range size of puku and lechwe in each of the seasons.

1.11 Hypotheses

1.11.1 The diet of puku and lechwe will be comprised of different grass species. The diet of lechwe will be comprised mainly of hydrophilic wetland grasses, while

puku will feed on grazing tolerant, widely distributed, mesophytic floodplain grasses. Both the diets of puku and lechwe will be comprised of a low variety of grass species.

1.11.2 The level of dietary overlap between puku and lechwe will be high. Many grass species in the diets will overlap between puku and lechwe.

1.11.3 The grasses in the diets of puku and lechwe will have high acceptability values throughout the year.

1.11.4 The average height of grass species eaten by lechwe will be higher than that of puku because the grass species eaten by lechwe will be emergent and regenerating after periods of inundation and be in areas of high soil moisture. The average greenness of the grass species eaten by lechwe will be higher than that of puku because the grass species will be emergent and regenerating after periods of inundation whilst still being in areas of high soil moisture.

1.11.5 Grass species classified as staple, quality, and/or key resources will differ between the diets of puku and lechwe. The periods during which these resources are consumed will differ between puku and lechwe. Puku and lechwe will face critical nutritional periods at different times of the year. Levels of CP_f and faecal phosphorus will be lowest in puku when they feed in the shrublands during periods of maximum inundation of the floodplain. Lechwe will face critical nutrition levels during periods of minimum inundation of the floodplain when preferred interface and shallow swamp habitats have contracted to a minimum.

1.11.6 Resource selection functions for lechwe will attain higher values for habitats in areas recently exposed by receding water or in areas of shallow swamp (<1m). Resource selection functions for puku will be higher in habitats in dry, low lying areas of floodplains.

1.11.7 The RSF of habitats available to puku and lechwe will remain constant throughout the seasonal cycle. Resource selection functions for puku and lechwe habitats will not change throughout the year.

1.11.8 For security against predators, puku and lechwe will select habitats with low levels of visual obstruction. Lechwe will select habitats at close proximity to water as they often flee into water to escape predation.

1.11.9 The size of puku and lechwe population ranges will be the same in each of the seasons.

1.12 General approach

The data for the study were collected in ways which would facilitate statistical analyses. The general approach I used in this thesis was to begin by describing the diet of puku and lechwe. With knowledge of diet composition, I then analysed and compared the diet of puku and lechwe, with particular reference to seasonal changes in species selection. Using data collected on used and available habitat locations I then assessed and compared possible factors influencing seasonal habitat selection of puku and lechwe. Faecal pellets collected throughout the duration of the study provided information on the nutritional status of puku and lechwe. I described the results of the faecal analyses in relation to the species composition and quality of the diet over the seasonal cycle. Finally, a synthesis of the interplay between diet, habitat selection and nutritional status between puku and lechwe are given along with recommendations for further research. Specific methods used to obtain and analyse the data relevant to each section are given in the appropriate chapters. The same methods of herd and site selection were used to determine diet and habitat use and as such are described below.

Due to the lack of collars, puku and lechwe herds were located from a vehicle or boat through visual observations using a spotting scope. Each study site was numbered and progressively sampled on consecutive days (**Figure 6**). Study sites were then sub-divided into quarters, and each quarter was sampled according to a predefined order (**Figure 6**). Sampling in each quarter began at a consecutive number each week i.e. if sampling started in quarter 2 in the first week it then began in quarter 3 the

following week etc. If no puku or lechwe were found in the first quarter sampled then sampling progressively followed in each of the remaining quarters. Foraging sites and habitat types used by puku and lechwe were then sampled by walking to the location where the animals were sighted and collecting the appropriate data.

This study focused on sampling female foraging sites as they are the primary social unit of puku and lechwe. An average of two puku and two lechwe foraging sites were sampled per day of observation. Sampling took place during the mornings and an attempt was made to sample puku and lechwe populations at matching times so as to avoid bias in the data associated with possible differential diurnal behaviours of each species.

Field data collection spanned a period of approximately one year (June 2007 – May 2008). To asses changes in diet and habitat use over the seasonal cycle the data collection period was sub-divided into two seasons in accordance with the floods and rainfall (**Figure 4**, Dipotso & Skarpe, 2006): **Low water season** (September - February); **High water season** (March - August). The timing of the floods was dependent on rainfall in Angola. Thus, rainfall levels in Kasane did not coincide exactly with the level of the flood. Flood level in the study area could be high even if the region had not experienced rainfall for some time.

CHAPTER 2

DIET OF PUKU AND LECHWE ALONG THE CHOBE RIVER FLOODPLAINS OF NORTHERN BOTSWANA

2.1 Introduction

In Southern Africa, a large portion of ecological research has been committed to the diets of large mammalian herbivores (Owen-Smith & Novellie, 1982; McNaughton & Georgiadis, 1986; Owen-Smith & Cooper, 1987; Owen-Smith, 1994; Ben-Shahar, 1996; Macandza *et al.,* 2004; Knoop & Owen-Smith, 2006). The aim of these studies was to asses the resource selection, and/or dietary preference of the animal species under investigation. In environments where resources may be limited, the selection of food resources could be important in serving a basis for ecological separation of sympatric herbivores and may also be an important adaptation for the survival of intraspecific competitors (Duncan, 1975; Macandza *et al.,* 2004).

The overriding factors determining the diet of any animal are the nutrient requirements needed for growth and maintenance. Optimal foraging theory suggests a food item should be accepted if the benefit obtained from consuming it outweighs the cost of searching for and ingesting a more profitable food item within the time available (Stephens & Krebs 1986, in Owen-Smith 2005). Requirements may theoretically be met by either harvesting a minimal amount of highly nutritious food, or by consuming a larger amount of proportionally less nutritious food (Duncan, 1975).

Availability and quality of food resources for herbivores are not constant but vary both seasonally and spatially across savanna ecosystems (Bell, 1982; Walker, 1993; Macandza et al., 2004). During the annual growth cycle, grasses typically develop from a short leafy growth stage with high levels of nutrients to a tall, mature to

senescent stage with low nutrient concentrations (Dye & Walker 1987; Georgiadis & McNaughton 1990; Ben-Shahar & Coe 1992). Important nutrients such as nitrogen, a biologically important element for the formation of proteins and nucleic acids as well as the creation of energy (Sinclair, 1977; Berry & Louw, 1982; Ketelaars, 1986), and phosphorus, important for growth and reproduction (Grassman & Hellgren, 1993), decline and fibre levels increase as grasses become senescent (Owen-Smith, 1982). Such fluctuations in nutritional quality form the basis for the determination of critical periods in which grazing animals struggle to meet metabolic requirements.

Variation in quality and quantity of resources may allow the categorization of foods consumed by herbivores as follows (Owen-Smith 2005); *quality resources* - high quality foods/areas that provide high intake rates but generally have restricted accessibility; *staple resources* – foods that supply adequate levels of nutrition and provide the bulk of the diet for most of the season; *key resources* - resources of generally low quality and are less favoured by the animal but can sustain maintenance levels during critical periods.

The dry season is commonly suggested as being the period of greatest nutritional stress in African savanna grasslands (Western, 1975; Sinclair, 1977; Owen-Smith, 1982). However, environments such as floodplains, which have close proximity to water and high soil moisture content, could potentially allow forage resources to retain greenness and high nutritive quality throughout the year. However, the feeding activities of floodplain ungulates are strongly linked to the flood regime of the river along which they live (Rees, 1978 [a, b, c]; Goldspink *et al.,* 1998; Dipotso & Skarpe, 2006). Critical periods may therefore arise as flooding inundates resources and these become unavailable rather than diminished in quality. As animals move off floodplains into elevated areas to avoid the floods, the effect of rainfall may then become important as animals rely on dryland vegetation that may vary in composition and nutritional quality from those plant species commonly found on floodplains. Because flooding is coupled to the rainy season in Africa, floodplain ungulates may

face critical periods not during the dry season, but during the wet season when large portions of the floodplains become inundated.

During the favourable months, such as the low water season, preferred grazing resources are common and widely available on the floodplains with inter- and intra-specific competition being at a minimum (Williamson, 1990). During the unfavourable high water season, availability of preferred resources is at a minimum while inter- and intra-specific competition is at a maximum due to constriction of the available floodplain habitats. Animals may begin to accept a wider range of spatial scales and utilize species, patches or landscape units that were previously avoided or only lightly utilized during the low water seasons (Williamson, 1990). By the end of the high water season previously avoided resources (key resources) may begin to become depleted potentially leaving animals with a critical period in nutrition.

Two congeneric species of floodplain antelope that are possibly subjected to critical periods during the wet season are puku (*Kobus vardonii)* and lechwe (*Kobus leche*). A thorough description on the current distribution and population status of puku and lechwe is given in **Sections 1.1**, **1.2**, and **1.3**, of **Chapter 1**. As can be seen in these sections, puku within Botswana have a low population count and an extremely localized and isolated distribution compared to lechwe. Both puku and lechwe are grazers, although both species have been documented as periodically feeding upon sedges and dicotyledons (Child & Von Richter, 1969; Williamson, 1990; Mills & Hes, 1997). Grazers such as puku and lechwe, which have similar body size, and reportedly occupy similar habitats (Rees, 1978; Williamson, 1990; Dipotso & Skarpe, 2006), could be expected to have similar diets. Describing the diets of these sympatric species thus becomes an important factor in the determination of ecological separation as well as explaining the context of intraspecific competition (Duncan, 1975).

The low population size and extremely localized distribution of puku within southern Africa highlight the urgent need for study and conservation of this species. It is in this light that the Botswana Department of Wildlife and National Parks have expressed concern towards puku, and have expressed a need to understand how to conserve the local population. In this chapter I investigated possible changes in the diet and nutritional status of puku and lechwe over a one-year period, and assessed dietary overlap between the two species. I hoped to highlight any significant differences or similarities between the two species that may indicate possible reasons for the limited distribution and low population size of puku in southern Africa compared with the more widespread and abundant lechwe.

2.2 Objectives

My objectives were to: **1)** to determine the level of dietary composition and overlap between puku and lechwe across seasons; **2)** determine a value of preference/acceptance for grass species in the diet of puku and lechwe; **3)** identify relationships between the structure and phenological condition of plant species in the diet and the animal preferences for these plants; and **4)** using faecal nutrient analyses, identify nutritionally critical and nutritionally stable periods for puku and lechwe.

2.3 Hypotheses

My hypotheses for this chapter were: **1)** the diet composition of puku and lechwe are similar, and share high levels of overlap across all seasons; **2)** acceptance values for grasses within the study sites are high because of the low number of grass species in the diets; **3)** grass greenness and height would influence preference of grass species. Greener grasses would have higher preference values than brown grasses. Puku and lechwe have relatively small mouths, and as such, taller grass swards would attain higher preference values because bite mass and thus ingestion rates would be increased; **4)** faecal nutrient values would be at a minimum during the high water

season for both puku and lechwe. The high water season would be the period during which puku and lechwe faced a critical period in nutrition. Faecal nutrient levels would be at a maximum during the low water season. The low water season would therefore be the season during which puku and lechwe faced a nutritionally favourable period.

2.4 Materials and methods

2.4.1 The study area

A detailed description of the study area is given in **Section 1.8** of **Chapter 1**.

2.4.2 Definitions and terminology

Distinctions in terminology are often neglected within the literature with many ecological studies using 'selection' and 'preference' interchangeably with little consideration for the specific definitions of the words (see for example Westoby, 1974, Parsons, 1994, and Baumont *et al.,* 2004). To reliably study the diet selection of an animal, it is necessary not only to have information on the proportions of the components in the diet, but also on the proportions of those components available to the animal. Dietary selection of a plant species can be defined as occurring when that plant species forms a significantly larger proportion of the diet than the proportion available in the section of the environment encountered by the animal while foraging. Negative selection or avoidance of a plant species can then be said to occur if a plant species is utilized in a significantly lower proportion to that which is available in the environment. Preference of a plant species by an animal is defined as occurring when that animal specifically chooses plant species 'A' over plant species 'B' when both species are equally available within the environment. But, since food types are never equally available in the wild, it must be remembered that the given definition of preference can only strictly be expressed in the context of a laboratory environment.

In practice, the use of a frequency of acceptance values may be far more beneficial to the researcher by giving a value of preference of a plant species based on the availability of that plant. Frequency of acceptance values relate the number instances in which a herbivore feeds on a particular plants species to the number of encounters with that plants species (see section 2.5.3.3 for specific calculations) in a given period.

The two methods I have chosen to use in determination of the dietary composition of puku and lechwe are direct observation (the bite-count method) and microhistological faecal analysis. Using direct observation allows the observer to compare the proportion of bites on a given plant species to availability in order to assess selectivity (Duncan, 1975). However, direct observation does not allow for accurate assessment of the ingested proportions of each grass species in the diet as it is not possible to determine variations in bite size between plant species in a recently grazed patch. Microhistological faecal analysis is therefore used in conjunction with direct observation in order to estimate, with minimum bias, the ingested proportions of grass species in the diets of puku and lechwe. Microhistological faecal analysis is not without its own bias however. Results may be affected by the extent of digestion of plant epidermis as it passes through the alimentary tract of a ruminant (Stewart, 1967; Slater & Jones, 1971; McInnes *et. al.* 1983; in Leslie *et. al.* 1983), with more readily digested grasses being underestimated in the faeces while less readily digested grasses are overestimated in the faeces (Brand, 1978). By supplementing direct observation and microhistological analysis with each other, I hoped to reduce the extent of bias in each method.

2.4.3 Data collection

2.4.3.1 Direct observation

Each of the intensive study areas was divided into 4 sub-units (**Figure 6**). Each of the sub units were then sampled consecutively until puku or lechwe were located. Sampling began in a different sub unit on each day of sampling within each of the intensive study sites. Puku and lechwe herds were located each morning between 06h00 and 11h00 using an Elite 80mm, 10-60 times magnification spotting scope or Zeiss 8x56 binoculars. A Bushnell Yardage Pro 400 laser range finder was then used to determine the exact distance from the observer to the herd. At the location of the herd, a foraging site was determined by the presence of spoor, droppings and freshly cropped grass. A foraging site was defined as the entire area where the animals were observed to have been feeding for at least 15 minutes (Magome *et al.,* 2008). Foraging sites were considered independent of one another when separated by a minimum distance of 200 meters. At each foraging site, a feeding site was identified by freshly cropped grass. To avoid the risk of puku and lechwe foraging sites being altered by other animals, these areas were sampled immediately after the focal species had ceased to forage or moved away.

A quadrat (0.7 m x 0.7 m) was placed over an area of freshly cropped grass and each species was noted and identified. A further eight quadrats were placed within the foraging site; two in each of the cardinal directions around the first quadrat (**Figure 9**). Each quadrat was placed 2 m apart from the other quadrats. If no grazing was evident inside the quadrat but was evident just outside, then the quadrat was allowed to be 'flipped' once to incorporate the grazing. If no evidence of grazing was found in 5 of the 9 quadrats, then a further 4 quadrats were evaluated for grazing. The additional 4 quadrats were placed in diagonal directions to the first quadrat (**Figure 9**).

Within each quadrat each grass species present was recorded as well as the number of grazed and ungrazed grass tufts. If it was noticed that a grass species (e.g. *Cynodon dactylon*) had stolons (runners), those stolons were considered part of the parent tuft if secondary shoots were devoid of flowering structures. Secondary shoots with flowering structures present were considered to be independent plants. In the field the various species of the genus *Eragrostis* could not be accurately distinguished from one another and were thus classified by genus as *'Eragrostis* species*'*. Values from each of the nine quadrats were then summed to give the total number of grazed and ungrazed tufts of each grass species at each independent foraging site.

The relative percentage greenness of the grazed and ungrazed grass tufts was estimated visually for each species recorded within each quadrat. Estimations of greenness were made on the proportion of leaves that were green. Estimations of grass greenness were made using a Walker 8-point scale (Walker, 1976; see **Table 1**, **Appendix 1**). Once it was determined which greenness class a grass tuft belonged to, the mid-value of that class was used to represent the greenness of that tuft i.e. if a grass tuft was determined to be in the 51-75% greenness class of the Walker 8-point scale, that grass tuft was recorded as having 63% greenness. Using the mid-value of a greenness class had the advantage of converting greenness measurements from a categorical variable to a continuous variable, which simplified interpretation and analyses in some cases. Grass greenness values of each grass species were averaged for each foraging site by summing the greenness values of a grass species across all nine quadrats, and dividing this by the total number of tufts of that species within the foraging site.

The height of each bite on grazed portions of grass tufts were measured for each grass species within each quadrat. Measurements were made from the base of the grass to the lowest recognizable bite. Similarly, the height of each ungrazed grass tuft was measured for each grass species recorded in each quadrat. Measurements were made from the base of the grass to the tip of the tallest ungrazed leaf. The average height of the grazed tufts of each grass species were calculated for each foraging site by

summing the values of the grazed tufts of species 'A' and dividing this by the total number of grazed tufts of species 'A' across all nine quadrats. The average height of the ungrazed tufts was calculated in the same manner mentioned above. All height measurements were made using a 3 m tape measure, and recorded in millimeters. Recording the relative greenness and average height of the grazed and ungrazed grass tufts highlighted possible diet selection factors important to lechwe and puku.

2.4.3.2 Faecal analyses

Any fresh (< one day old) faecal pellets found at a foraging site were collected into paper bags. If more than one faecal sample from a particular herd was found at a foraging site, all samples were pooled to give a more representative assessment of the diet. Samples were then air-dried and shaded from direct sunlight and rainfall to avoid leaching of nutrients. The collected faecal pellets were then used for the following purposes:

i) Microhistological faecal analyses: Microhistological faecal analyses were performed following the procedures of Stewart *et al.* (1967), Bartolome *et al.* (1998), and O'Shaughnessy (2006 unpub.). Once dry, the faecal pellets were ground in a pestle and mortar. One gram of ground faecal matter was added to 5 ml of 70% concentrate hydrochloric acid (HNO_3). The suspension was then heated in a boiling (102˚C) water bath for 2-3 minutes. The resultant solution was diluted to a volume of 100 ml by the addition of water and reheated for a further 2-3 minutes to complete the clearing process (Stewart *et al.,* 1967; Bartolome *et al.,* 1998).

The solution was then poured through a 1 mm filter to prevent any bias in identification associated with large, less digested particles. Finally, the solution was spread onto a microscope slide and each prepared slide was transversed from the top edge of the slide to the bottom until 50 identifiable fragments were recorded. To aid

in identification, reference slides of all the grass species encountered in puku and lechwe feeding areas were prepared and mounted using the same methods listed above. As with field identifications, species from the *Eragrostis* genus could not be reliably distinguished from one another and were classified as *Eragrostis* spp.

ii) Faecal nutrient analyses: Faecal samples not used for microhistological analyses were analysed for faecal nitrogen and phosphorus concentrations so that critical periods in nutrition could be determined. All collected faecal samples were sent to the ARC Institute for Soil, Climate and Water laboratory, in Pretoria, South Africa where atomic absorption spectroscopy was used for analyses (Varian Inc., USA; Stowe, 2003). This method used the absorption of light to measure the concentration of gas-phase atoms. Faecal samples were vaporized, following which a beam of ultra-violet light was passed through the vapour. The resultant light passing through the vapour was detected and concentration measurements were calculated from standards of known concentration for nitrogen and phosphorus.

2.4.3.3 Comparison of dietary proportions derived from direct observation to microhistological fecal analyses.

To check for consistency and accuracy in observations, the results from direct observation were compared to the results from microhistological faecal analyses. Ratios of seasonal means obtained from direct observation and faecal analyses were calculated along with their respective confidence intervals. Confidence intervals of ratios overlapping 1 indicated that there was no significant difference between values obtained from direct observation and values obtained from faecal analyses. Confidence intervals that did not overlap 1 indicated that there was a significant difference between the values obtained from the two methods. All statistical calculations and analyses were performed using SPSS version 10.0 (SPSS Inc., Chicago, Illinois, U.S.A) and Statistica (Stat Soft Inc., Tulsa, Oklahoma, U.S.A.).

2.4.4 Data analyses

2.4.4.1 Determining the diets of puku and lechwe

i) Diet determination from direct observation: To estimate the seasonal mean dietary contribution of each grass species in the diets of puku or lechwe, each foraging site was considered an independent sampling unit. The proportional dietary contribution of each grass species at each foraging site was calculated by dividing the number of grazed tufts of each species by the total number of grazed tufts of all grass species within that foraging site. Grass species not occurring at a foraging site were recorded as 0 within that site. To obtain the seasonal dietary contribution of each grass species, the dietary proportions obtained from each foraging site were averaged across each season - by summing the proportions of each grass species and dividing this by the total number of foraging sites sampled within that season. Since proportional values are bounded between 0 and 1, and hence are not distributed normally, all proportions were arcsine transformed prior to statistical analyses.

ii) Diet determination from microhistological faecal analyses: To estimate the seasonal mean dietary contribution of each grass species in the diets of puku or lechwe, each foraging site was considered an independent sampling unit. The proportional dietary contribution of each grass species from each faecal sample (foraging site) was calculated by dividing the total number of identified fragments of each species by 50 - the total number of identified fragments per faecal sample. Grass species not occurring within a faecal sample were recorded as 0. To obtain the seasonal dietary contribution of each grass species, the dietary proportions obtained from each faecal sample were averaged across each season - by summing the proportion of each grass species and dividing this by the total number of faecal samples within that season. All proportions were arcsine transformed prior to analyses.

2.4.4.2 Determining the level of dietary overlap between puku and lechwe

The degree of dietary overlap between puku and lechwe was assessed using Pianka's Niche Overlap Formula (Pianka, 1973 cited in Fritz *et al.*, 1996):

$$O_{jk} = \frac{(\sum U_{ij} * \sum U_{ik})}{\sqrt{(\sum U_{ij}^2 * \sum U_{ik}^2)}}$$

Where:

U_{ij} was, for example, the proportion of grazed grass tufts of puku (*j)* which were recorded in grass species (*i)*

U_{ik} was, for example, the proportion of grazed grass tufts of lechwe (*k)* which were recorded in grass species (*i)*

This index shows the degree of diet overlap, and may vary from 0 (indicating no diet overlap and complete resource partitioning), to 1 (indicating complete overlap of diets). The index was calculated in each of the four seasons to establish patterns of overlap change over the course of a year.

2.4.4.3 Acceptability and availability

Merely stating selection or avoidance of a resource does little in the way of classifying resource units in terms of their acceptance to large herbivores. Some index of preference is therefore needed to measure relative preference of vegetation to herbivores. Owen-Smith & Cooper (1987) used acceptance or rejection frequencies of woody vegetation to asses the preferences of greater kudu (*Tragelaphus strepsiceros*) by deriving frequency of acceptance values in the range of 0 to 1. Thus, food resources that were avoided or neglected attained a value of (or

close to) 0, with foods that were more readily accepted lying at the upper end of the scale attaining a value of (or close to) 1.

Individual grass tufts fed upon within a feeding location may not be considered to be selected independently from one another. Acceptance frequencies based on individual grass tufts (plant-based acceptance) may therefore be misleading by overestimating the relative acceptance frequency of certain grasses. Due to the nature of the calculations (see 2.5.3.3 ii), acceptance frequencies calculated at the foraging site level may also lead to misleading conclusions, e.g., a grass species with one tuft fed upon is recorded the same as a grass species with 10 tufts fed upon. Since there is no ideal measure of acceptance, and since the measure of acceptance depends on the definition of the feeding opportunity, both plant-based and site-based acceptances have been included in this chapter to supplement one another and give a clearer indication of the acceptance values of grasses. In section 2.5.3.3 iii, site-based acceptance was used to assess relationships between acceptance and grass phenology due to independence of the site-based values.

It may be misleading to present values from plant-based and site-based acceptance using the same values of low, medium, and high acceptance. This is because plant-based acceptance values are inherently lower than site-based acceptance values (Owen-Smith & Cooper 1987). Plant-based acceptance values were defined as such; favoured grass species attained a FOA $\geq$0.35, intermediately accepted grasses attained a value of 0.1 $\leq$ FOA < 0.35, and neglected species attained a FOA <0.1. Site based acceptance values were defined as; favoured grass species attained a FOA $\geq$0.5, intermediately accepted grasses attained a value of 0.2 $\leq$ FOA < 0.5, and neglected species attained a FOA <0.2.

i) Plant-based acceptance and availability: Plant-based acceptances of grass species were determined using a modification to the methods of Owen-Smith & Cooper (1987) and highlighted the likelihood of a grass species being fed upon when

within neck reach of a puku or lechwe. Neck reach was defined from observations on impala (Owen-Smith & Cooper, 1987), a similarly sized animal to puku and lechwe, as a distance of 0.35m on either side of hoof placement. Each foraging site was considered an independent sample. Plant-based frequencies of acceptance values were calculated by dividing the number of grazed tufts of a particular grass species by the total number (grazed + ungrazed) of tufts of that species within each foraging site. Seasonal plant-based frequency of acceptance values were then calculated by summing the FOA values of each grass species and dividing this by the total number of foraging sites in which that grass species occurred within each season. These indices were restricted to a frequency of acceptance range between 0 (no acceptance or avoidance) and 1 (acceptance on each encounter i.e. preferred species). Plant-based availabilities were calculated by dividing the number of tufts of a particular grass species by the total number of tufts of all grass species within that foraging site. Seasonal plant-based availabilities were then calculated by summing the availabilities of each grass species and dividing this by the total number of foraging sites sampled in each season. Pearson's correlation coefficient was used to determine if there was any correlation between plant-based acceptance and plant-based availability for grass species occurring in ≥10 sites in each season. Analysis of grass species occurring in <10 sites could not be validated statistically. Since availability and acceptance values are bounded between 0 and 1, and do not have a normal distribution, values were arcsine transformed prior to statistical analyses. Using an arcsine transformation showed improved normality of the data over the square-root and log transformations. Statistical significance was set at $P \leq 0.05$.

ii) Site-based acceptance and availability: Site-based acceptance values of grass species were calculated by dividing the number of foraging sites where each grass species was grazed by the total number of foraging sites in which the grass species occurred in each season. Site-based availability of each grass species was determined by dividing the number of feeding sites where the grass species was present, by the total number of feeding sites sampled, in each season. Pearson's correlation

coefficient was used to determine if there was any correlation between site-based availability and site-based acceptance. All values were arcsine transformed prior to statistical analyses.

iii) Comparison of puku and lechwe in availability and acceptance of grass species, and factors affecting acceptability of grass species: To discriminate between puku and lechwe in regards to site-based acceptability, binary logistic regression was used to compare frequencies of grazing (coded as '1' for acceptance) or not grazing (coded as '0' for not accepted) in relation to grass species, grass height, the number of grass tufts, and grass greenness, for each grazer in each season. For the categorical variable grass species, only grasses that were present in ≥10 foraging sites for both puku and lechwe were entered into the regression. The interpretation of results for the grass species variable was in terms of a reference category which was set as *C. dactylon* for the LWS, and *A. macrum* for the HWS. Thus, the parameter estimates for the categorical dummy variables referred to the change in log odds when the dummy variable was equal to 1 (being selected), compared to the reference category equaling 1. For example, the odds ratio for *A. macrum* indicated the odds of that species being selected relative to the odds of *C. dactylon* being selected during the LWS. The remaining variables; grass height, number of tufts, and grass greenness, were entered as continuous variables. Data for grass height, number of tufts, and grass greenness, were entered from all grass species. By not discriminating between grass species this allowed me to independently asses the specific influences of grass height, greenness, and the number of tufts, on acceptability. The forward stepwise logistic procedure was used, with limits for entry and removal of variables set to $P = 0.1$ and $P = 0.2$ respectively. The dependent variable was acceptance (grazed or ungrazed) with grass species, grass height, number of tufts, and grass greenness being the covariates. The best model was assessed in terms of the Hosmer & Lemeshow chi-square statistic.

Site-based availability, of each grass species occurring in ≥10 foraging sites of both puku and lechwe, was compared between animal species, in each season, using univariate analyses of variance. The dependent variable in the model was availability, and the factor was species. Since availability values are bounded between 0 and 1, and do not have a normal distribution, availabilities were arcsine transformed prior to statistical analyses. Statistical significance was set at $P \leq 0.05$. Pearson's correlation test was then used to determine if there was any correlation between site-based acceptance and site-based availability for all grass species occurring in ≥10 foraging sites, for either puku or lechwe, in each season. All statistical calculations and analyses were performed using SPSS version 10.0 (SPSS Inc., Chicago, Illinois, U.S.A) and Statistica (Stat Soft Inc., Tulsa, Oklahoma, U.S.A.).

2.4.4.4 The influence of grass greenness and height in foraging site selection

The ungrazed tufts of grass swards were used as surrogates representing the condition of foraging sites prior to utilization by puku or lechwe, because they were largely unaffected by the foraging activities of either species. Measurements made on the ungrazed grass tufts were used as indicators of grass greenness and grass height for potential/available foraging sites. The ungrazed values of grass greenness and height were compared, between puku and lechwe, between seasons, using univariate ANOVA, to determine potential differences in selection of available foraging sites with regard to greenness and height. Grass greenness, or grass height, were the dependent variables used in the models, with grazer and season being the independent variables. The models were; grass greenness x species x season, and grass height x species x season. The level of significance was set at $P \leq 0.05$.

2.4.4.5 Fecal nutritional analyses

Mean seasonal faecal nitrogen and phosphorus values were calculated by averaging all values obtained for each season. Faecal nitrogen and phosphorus were compared between seasons for puku and lechwe using one-way ANOVA. Nitrogen or phosphorus was the dependent variable with season being the factor. Significance was set at $P \leq 0.05$. Faecal nutrient levels were compared between puku and lechwe between seasons by plotting seasonal nutrient means and confidence intervals from both species and determining whether confidence intervals overlap. Any overlap of confidence intervals indicated that there was no difference between faecal nutrient levels within that season. All results are presented as a percentage of the dry mass (DM) of a sample.

2.5 Results

2.5.1 The diets of puku and lechwe

i) Diet determination from direct observation: Over the course of one year, 21 grass species were recorded in the diet of puku and 17 in the diet of lechwe (for a full list of grass species recorded in the diets of puku and lechwe please see **Table 1, Appendix 2**). Puku fed on a total of 18 grass species during the LWS, and 16 grass species during the HWS. Lechwe fed on a total of 14 grass species during each of the LWS and HWS respectively.

Low water season **–** Puku fed on a total of 18 grass species during the low water season (**Figure 10**). Of the 18 grass species eaten by puku, just 3 of these species (*C. dactylon, D. eriantha,* and *V. nigritana*) made up 54.2% of the seasonal diet. Lechwe fed upon 14 grass species during the LWS (**Figure 10**). Three of these grass species (*C. dactylon, D. eriantha, P. mauritianus*) contributed 62.1% of the diet of lechwe during the LWS. Puku and lechwe overlapped in the use of *C. dactylon,* and *D.*

eriantha, each of which were among the grass species contributing >10% to the diets of both species. The contribution of *C. dactylon* was greater in the diet of lechwe (30.6%) than in the diet of puku (25.6%). *Digitaria eriantha* formed a greater contribution to the diet of puku (12.2%) than the diet of lechwe (10.2%). However, the dietary contributions of *C. dactylon* and *D. eriantha* were not significantly different between puku and lechwe. Differences in grass species composition between puku and lechwe during the LWS include *A. adscensionis, B. eruciformis, C. gayana, D. aegyptium, S. pyramidalis,* and *S. sphacelata* which were only consumed by puku and only during this season. These grass species formed a total dietary contribution of just 3.6%. *Aristida stipitata* and *Echinochloa colona* were only eaten by lechwe during the LWS, and these species only contributed 2.9% of the diet.

High water season – Puku consumed 16 grass species during the HWS (**Figure 10**). Four of the 16 grass species consumed by puku during the HWS; *A. macrum, C. dactylon, D. eriantha,* and *Eragrostis spp.,* contributed a combined total of 60.9% of the diet. The seasonal dietary contributions of *C. dactylon* and *D. eriantha* remained fairly constant from the LWS (25.6% and 12.2% respectively) to the HWS (25.8% and 11% respectively). *Acroceras macrum* and *Eragrostis spp.* both slightly increased in dietary contribution to 12.9% and 11.2% respectively, during the HWS. *Vetivera nigritana* decreased from the LWS to the HWS, with its dietary contribution dropping from 16.4% to 6.2%. The dietary breadth of lechwe remained constant from the LWS to the HWS, with 14 grass species being fed upon (**Figure 10**). Similar to the LWS, only 3 grass species (*A. macrum, C. dactylon,* and *P. mauritianus*) contributed 75.7% of the diet of lechwe during the HWS. *Acroceras macrum* more than doubled from the LWS (9.6%) to the HWS (21%). *Cynodon dactylon* also increased in during the HWS, contributing 39.9% of the diet. The dietary contribution of *P. mauritianus* decreased from 21.3% during the LWS to 14.8% during the HWS. *Digitaria eriantha* decreased in the diet of lechwe from contributing 10.2% of the diet during the LWS to just 2.8% during the HWS. Of the grass species with seasonal dietary contributions of ≥10% during the HWS, puku and

lechwe overlapped in the use of *A. macrum* and *C. dactylon.* Both of these grass species formed greater contributions (difference of 8.1% and 14.1% respectively) to the diet of lechwe.

The individual annual contributions of *A. macrum, C. dactylon, D. eriantha,* and *V. nigritana* were ≥10% in the diet of puku. Combined these four grass species formed 59.9% of the annual diet. Annually, *C. dactylon* contributed more than double any of the other grass species, with an annual contribution of 25.6%. Annually, lechwe fed upon a narrower range of grass species. In the annual diet of lechwe just 3 grass species (*A. macrum, C. dactylon,* and *P. mauritianus*) formed 67.7% of the diet. Similar to puku, the greatest single annual contributor to the diet of lechwe was *C. dactylon* (34.7%), providing nearly double that of the next greatest contributor, *P. mauritianus* (18.4%).

ii) Diet determination from microhistological faecal analyses and comparison to results from direct observation: A full list of the results from microhistological faecal analyses can be seen in **Table 1, Appendix 2**. Microhistological faecal analyses were used in this study to supplement and support the findings from direct observations. Minor differences were detected between the two methods in the number of grass species eaten by puku and lechwe. Microhistological analyses identified puku as feeding on a total of 20 grass species compared to 21 grass species identified from direct observation. Lechwe consumed a total of 16 grass species identified through microhistological analyses compared to 17 identified through direct observation.

Slight seasonal variations were also observed between the seasonal grass species composition of the diets of puku and lechwe. Grass species identified as being in the diet by one method and not the other (*S. pyramidalis* and *S. sphacelata* through direct observation; *B. nigropedata, P. repens,* and *T. triandra* through faecal analyses), had a total contribution of just 4.3% of the seasonal diet..

Low water season – Faecal analyses identified puku as feeding upon 19 grass species during the LWS (**Figure 10**). Only 2 grass species were identified as having seasonal dietary contributions of ≥10%. *Cynodon dactylon* and *A. macrum* contributed 32.5% of the LWS diet of puku. Confidence intervals calculated around dietary proportions of grass species in the diet of puku showed little correlation between estimates obtained from direct observation and estimates obtained from faecal analyses (i.e., no overlap of confidence intervals, **Table 1, Appendix 2**). Of the 21 grass species identified through both methods as being in the diet of puku, ten grasses had mean seasonal dietary proportion estimates that were significantly higher when determined through direct observation compared to faecal analyses. Nine grass species had mean seasonal dietary proportion estimates that were significantly lower when determined through direct observation compared to faecal analyses. Of the grass species identified as contributing ≥10% to the diet in each method, only *A. macrum* did not differ significantly between the two methods of observation. The remaining grass species contributing ≥10% to the diet - *C. dactylon, D. eriantha,* and *V. nigritana,* had significantly higher dietary proportions when estimated through direct observation, compared to faecal analyses.

Fourteen grass species were identified, through faecal analyses, as contributing to the diet of lechwe during the LWS (**Figure 10**). Four grasses had seasonal contributions of ≥10% in the diet of lechwe during the LWS. *Acroceras macrum, C. dactylon, P. mauritianus,* and *V. nigritana* contributed 61.1% of the diet of lechwe during the LWS. Observations made on the diet of lechwe through direct observation and faecal analyses were more closely matched than those of puku. Significant differences in dietary contributions, determined through both methods, were seen in 7 of the 16 grass species recorded in the diet of lechwe during the LWS, compared to 19 out of 21 grass species recorded in the diet of puku (see CIs in **Table 1, Appendix 2**). From the grass species contributing ≥10% to the diet of lechwe, only *C. dactylon* differed significantly between direct observation and faecal analyses. The estimate of the contribution of *C. dactylon* to the diet of lechwe was higher when determined through direct observation (30.6%) compared to faecal analyses (19.9%).

High water season – Microhistological faecal analyses identified puku as feeding on 13 grass species during the HWS, 6 less than the LWS (**Figure 10**). Four grass species; *A. macrum, B. eruciformis, C. dactylon,* and *D. eriantha,* had seasonal dietary contributions ≥10%, with a total dietary contribution of 73%. As in the LWS, dietary values calculated from direct observation correlated little with values from faecal analyses. From the 17 grass species, identified from both methods, in the diet of puku, 10 grasses differed significantly in their seasonal estimates. Three grass species had significantly lower, and 7 grasses had significantly higher dietary proportions when estimated through direct observation compared to faecal analyses (see CIs in **Table 1, Appendix 2**). *Acroceras macrum* was the only grass species contributing ≥10% to the diet of puku that did not differ significantly between direct observation (12.9%) and faecal analyses (12.7%). Direct observation gave significantly higher estimates than faecal analyses for the dietary proportions of *C. dactylon* and *Eragrostis spp.,* both of which had seasonal contributions of ≥10%. The dietary contribution of *D. eriantha* was significantly lower when estimated through direct observation (11%) compared to faecal analyses (19%).

Faecal analyses showed lechwe to feed upon 13 grass species during the HWS (**Figure 10**). Three grasses, *C. dactylon, P. mauritianus,* and *V. nigritana,* had seasonal contributions of ≥10% in the diet of lechwe during the HWS. These 3 grasses had a combined total dietary contribution of 55.4%. Discrepancies between direct observation and faecal analyses were more pronounced during the HWS compared to the LWS. Of the 13 grass species recorded in the diet of lechwe, 9 differed significantly in dietary proportion estimates between direct observation and faecal analyses (see CIs in **Table 1, Appendix 2**). Four grass species had significantly higher and 5 grass species had significantly lower dietary estimates when determined from direct observation compared to faecal analyses. From the grass species contributing ≥10% to the seasonal diet, no significant difference was detected between analyses methods for *P. mauritianus.* The dietary contribution of *C. dactylon* was significantly higher when determined through direct observation

(39.9%) compared to faecal analyses (22.3%). The dietary contribution of *V. nigritana* was severely underestimated when calculated from direct observation (1.4%) compared to faecal analyses (14.3%).

Despite results indicating high levels of inconsistencies between estimates obtained from direct observation and faecal analyses, sample sizes were greater from direct observation methodology. Greater statistical precision and confidence may be placed in results obtained from larger sample sizes compared to results obtained from smaller sample sizes. Values obtained through the methods of direct observation were therefore used for further analyses for the remainder of the chapter.

2.5.2 Dietary overlap

Dietary overlap was high in both seasons for puku and lechwe (**Figure 11**). The total contributions of *C. dactylon, D. eriantha,* and *A. macrum* to the diets of puku and lechwe were 46.1% and 40.4% respectively. The dietary contributions of these grasses appear to account for the high level of dietary overlap between puku and lechwe during the LWS. During the HWS, *A. macrum, C. dactylon,* and *Eragrostis spp.* each contributed greatly to the diets of puku and lechwe, forming 49.9% and 69.5% of the diets respectively, thereby accounting for the high level of dietary overlap between the species during this season. The level of dietary overlap increased from the LWS to the HWS. The increase in the level of dietary overlap was mirrored by the increase in the dietary contributions of *A. macrum* and *C. dactylon* in the diets of puku and lechwe from the LWS to the HWS. The level of dietary overlap therefore appeared to be strongly linked to the relative contributions of *A. macrum* and *C. dactylon* in the diets of puku and lechwe.

2.5.3 Acceptability and availability

i) Plant-based acceptance and availability

Low water season - During the LWS, 7 grass species were found to be highly acceptable to puku (**Figure 12**). Each of the highly accepted grass species; *A. adscensionis, B. humidicola, C. gayana, D. aegyptium, S. pyramidalis, S. sphacelata,* and *V. cuspidata* had availabilities of ≤1% (**Figure 13**). Of the 3 grass species with high dietary contributions (contributing ≥10% to the seasonal diet of puku), both *C. dactylon* and *D. eriantha* were found to be intermediately accepted ($0.1 \leq FOA < 0.35$) by puku during the LWS despite having high availabilities of 27.4% and 11.5% respectively. Although *V. nigritana* was the second most available grass species to puku during the LWS, contributing 17.4% of the grasses available, it was also only intermediately accepted. Just 2 grasses were highly accepted by lechwe during the LWS; *E. colona* and *V. cuspidata* (**Figure 12**). Both of these highly accepted species had availabilities of <3% (**Figure 13**). Despite some grasses such as *Cynodon dactylon, A. macrum, D. eriantha, P. deusteum,* and *P. mauritianus* having high availabilities, the remainder of the grass species in the diet of lechwe were only intermediately accepted. There was no correlation between acceptance and availability ($P > 0.05$) of grasses in the diets of either puku or lechwe during the LWS.

High water season – Six grass species were highly accepted by puku during the HWS (**Figure 14**). Of the 6 highly accepted grass species, *B. eruciformis* and *B. humidicola* had the highest availabilities of 7.7% and 6.2% respectively (**Figure 15**). The remaining favoured grass species; *B. dura, C. gayana, E. colona,* and *P. repens* had availabilities of ≤2%. *Acroceras macrum, C. dactylon, Eragrostis spp.,* and *D. eriantha* all had dietary contributions and availabilities of ≥10%, and each were intermediately accepted by puku during the HWS. Two grasses, *P. mauritianus* and *P. scrobiculatum,* were neglected by puku during the HWS. Lechwe highly accepted *D. eriantha* and *S. sphacelata* during the HWS despite both grasses having availabilities of <3% at lechwe foraging sites (**Figures 14** and **15**). The grasses with

the highest availabilities at lechwe foraging sites were *A. macrum* (20%), *C. dactylon* (39.2%), and *P. mauritianus* (14.2%), and each of these species was intermediately accepted by lechwe during the HWS. With an availability of 3%, *P. scrobiculatum* was the only grass neglected by lechwe during the HWS. Pearson's correlation coefficient showed *C. dactylon* (*Pearson Correlation Coefficient* = -0.517, $P = 0.020$) to be the only grass species that had correlation between acceptance and availability. The correlation was negative, indicating that as availability increased, acceptance decreased. No significant correlation ($P > 0.05$) was detected between acceptance and availability for the remaining grass species in the diets of puku or lechwe during the HWS.

ii) Site-based acceptance and availability

Low water season **-** Site-based acceptance values from both the LWS and HWS indicated most grasses in the diets of puku and lechwe to be highly accepted. All grass species in the diet puku during the LWS were highly accepted (**Figure 16**). *Cynodon dactylon* and *V. nigritana* had the highest availabilities at puku foraging sites during the LWS (**Figure 17**), and both grasses had acceptance values of ≥0.9. *Eragrostis spp.* and *D. eriantha* were the 3rd and 4th most commonly available grasses at puku foraging sites during the LWS, both with acceptance values of >0.75. At lechwe foraging sites during the LWS, the most commonly available grasses were *C. dactylon* and *P. mauritianus*. Frequency of acceptance values of these grasses were high, being ≥0.8 for both species. Similar to puku foraging sites, *D. eriantha* was the 4th most commonly available grass species at lechwe foraging sites. *Digitaria eriantha* was accepted by lechwe each time it occurred at a foraging site. The only grass species to be intermediately accepted by lechwe during the HWS was *V. nigritana.* Availability of *V. nigritana* was low during the LWS, being available at <10% of lechwe foraging sites.

High water season - Site-based frequency of acceptance values were again mostly within the highly acceptable range during the HWS (**Figure 18**). Five grass species

had site-based availabilities of >10% at puku foraging sites during the HWS (**Figure 19**). The most available grass species at puku foraging sites was *C. dactylon,* and it had an acceptance of 0.808. Of the grasses with availabilities of >10%, *A. macrum* was the most highly accepted grass species with an acceptance value of 0.909. *Brachiaria humidicola* and *D. eriantha* both had availabilities of 0.175 at puku foraging sites and both species attained acceptance values of ≥0.7. *Eragrostis spp.,* also with availability of >10% at puku foraging sites, had an acceptance value of 0.647. At lechwe foraging sites during the HWS, *Eragrostis spp.* and *P. mauritianus* both had availabilities of 0.135, and both species had an acceptance value of 0.778. The two most available grasses at lechwe foraging sites during the HWS were *A. macrum* and *C. dactylon,* and both species had acceptance values of >0.85.

Site-based acceptance was not correlated to site-based availability for neither puku (*Pearson's Correlation* = 0.204, *P* = 0.152) nor lechwe (*Pearson's Correlation* = 0.116, *P* = 0.460).

iii) Comparison of puku and lechwe in acceptance of grass species, and factors affecting acceptability of grass species

Low water season - *Cynodon dactylon* and *D. eriantha* were the only grass species that occurred in ≥10 foraging sites of both puku and lechwe during the LWS. The odds of puku accepting these grass species during the LWS decreased by 36% (*95% CI* = 0.940 to 0.989, *Odds ratio* = 0.964, *P* = 0.005) for every 10mm increase in grass height. None of the variables; number of tufts (*P* = 0.331), grass height (*P* = 0.991), grass greenness (*P* = 0.261), and grass species (*P* = 0.146), that were entered into the logistic regression procedure were found to have a significant relationship to acceptance by lechwe during the LWS.

High water season – *Acroceras macrum* and *C. dactylon* were the only grasses that occurred in ≥10 of the foraging sites of puku and lechwe during the HWS. The odds of puku accepting a grass species, during the HWS, decreased by 20% (*95% CI* =

0.964 to 0.997, Odds ratio = 0.980, P = 0.019) for every 10mm increase in grass height. A 10% increase in grass greenness increased the odds of acceptance by puku by 212% (*95% CI* = 1.010 to 1.453, Odds ratio = 1.212, P = 0.039), during the HWS. The only variable to have a significant impact on acceptance by lechwe during the HWS was grass height. The odds of acceptance by lechwe decreased by 37% (*95% CI* = 0.929 to 0.998, Odds ratio = 0.963, P = 0.040) for every 10mm increase in grass height during the HWS.

2.5.4 The influence of grass greenness and height in foraging site selection

Average grass height at puku foraging sites was an average of 173 mm (*SE* = 12.60) during the LWS and 286 mm (*SE* = 13.42) during the HWS (**Figure 20**, $F_{1, 386}$ = 31.938, $P < 0.001$). The average grass height at lechwe forging sites was 138 mm (*SE* = 15.61) during the LWS, and 269 mm (*SE* = 17.37) during the HWS (**Figure 20**, $F_{1, 179}$ = 43.077, $P < 0.001$). There was no significant difference in grass height between puku and lechwe foraging sites between seasons (**Figure 20**, $F_{1, 465}$ = 0.367, P = 0.545).

Average grass greenness at puku foraging sites was 71% (*SE* = 1.01) during the LWS and 80% (*SE* = 1.07) during the HWS (**Figure 21**, $F_{1, 286}$ = 28.174, $P <0.001$). During the LWS the average grass greenness at lechwe foraging sites was 74% (*SE* = 1.25), with grass greenness being on average 81% (*SE* = 1.39) during the HWS (**Figure 21**, $F_{1, 179}$ = 15.658, $P < 0.001$). There was no significant seasonal difference in the average greenness of selected foraging sites between puku and lechwe (**Figure 21**, $F_{1, 465}$ = 0.495, P = 0.482).

2.5.5 Faecal nutrient analyses

Puku faecal nitrogen levels did not differ significantly (**Figure 22**, $F_{1, 33}$ = 0.637, P = 0.431) between the low water and high water seasons. Puku faecal phosphorus levels

were significantly (**Figure 23**, $F_{1, 33}$ = 4.211, P = 0.048) different between the low water and high water seasons, being on average 0.27% DM (SE = 0.029) during the LWS and 0.35% DM (SE = 0.025) during the HWS. There were no significant differences between faecal nitrogen (**Figure 22**, $F_{1, 28}$ = 0.148, P = 0.704) or faecal phosphorus (**Figure 23**, $F_{1, 28}$ = 0.254, P = 0.618) levels for lechwe between the low water and high water seasons. Neither faecal nitrogen ($F_{1, 65}$ = 0.050, P = 0.824) nor phosphorus ($F_{1, 65}$ = 0.780, P = 0.381) varied significantly between puku and lechwe within seasons.

2.6 Discussion

The diets of both puku and lechwe along the Chobe River were composed exclusively of grass species. These findings differed slightly from those reported by Williamson (1990) and Mills & Hes (1997), both of which listed puku and lechwe occasionally accepting sedges and dicotyledons. The number of grass species identified in the diets of puku and lechwe was similar to those identified in other studies in Chobe (Child & Von Richter 1969; Von Richter & Osterberg 1977) and the Linyanti Swamps (Rees 1978).

Associated with the rise of the flood-waters was the inundation of the floodplains immediately adjacent to the Chobe River. As puku (Mills & Hes, 1997; Goldspink *et al.,* 1998; Dipotso & Skarpe, 2006) and lechwe (Rees, 1978; Mills & Hes, 1997) are floodplain grazers, the rise of flood-waters and the inundation of floodplains, should have signified the beginning of a period of stress for both species as the availability of preferred foraging habitat decreased. Although the quantity of available habitat in each season was not assessed in this chapter, it was clearly evident that the inundation of the floodplains pushed both species into habitats not favoured by either. An increase in the level of the flood-waters appeared to have an inverse effect on the availability of suitable foraging habitat. Both puku and lechwe were seen to congregate around the edges of the flood-waters and on islands of high-lying

grasslands within flooded areas, often feeding together in mixed herds. A consequence of the decrease in available habitat was the increase in the level of dietary overlap from the LWS to the HWS.

There have been no previously documented studies directly comparing the diets of species within the *Kobus* genus, but when compared to studies conducted on other animal species (see for example; Hansen & Reid 1975; Mysterud 2000; Macandza 2009), the levels of dietary overlap between puku and lechwe appeared to be high. During the LWS, the season when preferred habitat availability was assumed to be at a maximum due to low water level, dietary overlap was 84%, the lowest recorded level throughout the year. Dietary overlap increased from the LWS to the HWS, with puku and lechwe overlapping in 90% of their diets during the HWS.

The increase in the level of inundation of the floodplains was mirrored by an increase in the total dietary contributions of *A. macrum, C. dactylon,* and *Eragrostis spp.* to the diets of puku and lechwe. Availability of *A. macrum, C. dactylon,* and *Eragrostis spp.* remained high during the HWS while declines were recorded in the availability of *V. nigritana* and *P. mauritianus.* Both *V. nigritana* and *P. mauritianus* are hydrophytic grass species growing almost exclusively in floodplain habitats or shallow water (Van Oudtschoorn 1999). Dietary contributions of both these species were seen to decline drastically during the HWS, likely as a result of their decline in availability due to the inundation of the floodplains. Puku and lechwe appeared to compensate for the decline in availability of *V. nigritana* and *P. mauritianus* by increasing the dietary contributions of *A. macrum, C. dactylon,* and *Eragrostis spp.* The dietary contributions of *A. macrum, C. dactylon,* and *Eragrostis spp.,* appeared to be the main grass species influencing the level of dietary overlap between puku and lechwe in each season.

Despite high levels of overlap in both seasons, the diets of puku and lechwe differed somewhat in important features. In both seasons, puku and lechwe differed in the dietary contributions of *V. nigritana* and *P. mauritianus.* Annually lechwe consumed 2.3 times the quantity of *P. mauritianus* than did puku, while puku consumed 5.3

times the quantity of *V. nigritana* than did lechwe. As mentioned previously, both *V. nigritana* and *P. mauritianus* occur exclusively in floodplain habitats. Since the preferred habitats of puku and lechwe were observed to be within floodplains (see for example Rees, 1978; Mills & Hes, 1997; Goldspink *et al.,* 1998; Dipotso & Skarpe, 2006), the respective dietary contributions of *V. nigritana* and *P. mauritianus* may be a function of ecological resource partitioning of forage within those floodplains (Schoener, 1974).

A further difference in the diets between puku and lechwe, in each season, was the contribution of the *Brachiaria* species. The *Brachiaria spp.* increased substantially in the diet of puku from the LWS to the HWS. The increase in the contribution of the *Brachiaria* species matched the increase in availability of the grasses at puku foraging sites. The *Brachiaria* grasses therefore appeared to form an important contribution to the diet of puku during the HWS when the animals were forced into shrubland areas. Lechwe did not appear to shift the focus of their feeding in such a manner. Rather, lechwe appeared to increase the proportion in the diet of the major contributing grasses from the LWS i.e. *A. macrum, C. dactylon*, and *P. mauritianus*, which remained available in the floodplains that were not inundated during the HWS.

The acceptance of grass species by puku was strongly dictated by the height of the grass sward in both seasons. Shorter grass species generally attained higher FOA values in the diet of puku. The particular height of grasses selected by puku in each season may be an indication of conforming to optimal foraging theory. Since bite volume is a product of mouth width and bite depth, puku, which have comparatively small mouths, may be maximizing ingestion rates by selecting grass swards in the height region of 170 mm during the LWS and 290 mm during the HWS. The noticeable difference in the height of grasses selected between the seasons may be explained in two ways. Firstly, during the LWS, grazing pressure upon the floodplains was notably higher than in the upland areas. Species such as elephant, buffalo, zebra, hippo, warthog, and impala, were all seen grazing on a daily basis within the floodplains. This constant grazing pressure maintained a relatively short

grazing lawn within the floodplains, compared to the upland areas, throughout the LWS. Secondly, the LWS coincides with the dry season. Much of the grasses within the floodplains were unable to regenerate after grazing due to the lack of rainfall during the LWS. With the onset of the rains, grasses were able to regenerate and grow to heights in excess of those recorded during the dry LWS. As inland pans fill with water during the rainy periods, and as the floodplains become inundated, animals such as elephant, buffalo, zebra, and kudu, move away from the riverfront thus alleviating much of the grazing pressure during the HWS. The reduction in grazing pressure, coupled to rainfall, allows grasses to grow to heights far taller than possible during the LWS.

Grass height had no effect on the acceptance of grass by lechwe during the LWS. When the availability of preferred grass species was still high during the LWS, puku and lechwe overlapped in acceptance and diversity of grasses contributing to the diet. As availability of the commonly favoured grasses declined with the onset of the HWS, puku appeared to adapt by selecting grass species that were short and green, while lechwe became more selective of the height of commonly preferred grasses. Grass greenness within the floodplains remained high from the LWS to the HWS and therefore had little influence on food selection by lechwe. However, due to increased rainfall and decreased grazing pressure on the floodplains during the HWS, the average height of grasses was higher than during the LWS. Lechwe thus had to become selective of grass height during the HWS to be able to maintain ingestion rates experienced during the LWS.

Although the disparity in body size is likely to be too small to have detectable effects, it is possible that the difference in body size (Geist 1974) between puku (77kg) and lechwe (118kg) played a role in the variation in precision and tolerance in food niche. The morphology and function of the digestives systems of these con-generic species may also have influenced precision and tolerance in grasses. Puku, being smaller than lechwe, may have selected for higher quality green leaves during the HWS to meet the higher energy requirement relative to body mass. Lechwe appeared to have been less constrained by food quality, and able to accept grasses from wider

phenological stages in order to meet metabolic requirements. The narrower selection preference of puku for shorter, greener grasses fit the niche breadth theory, which predicts low density species to use a narrower range of resources than high density species (Brown 1984).

Puku grazed upon a range of grass species that was slightly wider than that of lechwe, but the site-based acceptability of most grasses did not differ between the two species. The difference in the dietary breadth of the two species may have been a result of the different number of sites sampled between puku and lechwe. Only *V. nigritana* differed in acceptability between puku and lechwe during the LWS, and *D. aegyptium* and *P. scrobiculatum* differed between grazers during the HWS. Sample size of these three grass species was low and thus differences in acceptability cannot be statistically validated. However, as shown by logistic regression, the acceptability of grass species by puku was influenced specifically by the height of the grass during the LWS, and the height and greenness of the grass during the HWS. Lechwe only became selective for shorter grasses during the HWS. This suggests that lechwe were more generalist in grass height and greenness during the LWS, when availability of the commonly favoured grasses were high, becoming more selective in grass height, during the HWS, as availability declined. It was evident that both species became more selective towards the phenological characteristics of grasses during the HWS. The increase in selectivity by both species during the HWS was probably due to the increase in grass height and greenness resulting from increased rainfall and decreased grazing pressure during this season.

Despite the differences in features influencing acceptance of grasses by puku and lechwe, these congeneric species could not be differentiated in features influencing the selection of foraging sites. In terms of grass height and greenness, both puku and lechwe selected foraging locations in taller, greener grass stands during the HWS. As is apparent from figure 4, the rise of the floodwaters coincided with the start of the rainy season. Foraging sites being located within taller and greener grass stands

during the HWS were likely a result of the increased growth and production of grasses in upland areas during this period, rather than a consequence of selection. The LWS generally coincided with the late dry season. The result of this was a greater concentration of elephant, kudu, sable, impala, warthog, hippo, waterbuck, giraffe, and buffalo along the floodplains. Increased grazing pressure and the destructive influences of trampling upon the floodplains would have lowered the average height of grasses within the floodplains. During the dry season, most grasses were senescent and brown in colour. With the onset of the rains, inland pans and watering holes began to hold water and attracted species such as buffalo, elephant, kudu, zebra, sable (*Hippotragus niger*), and giraffe (*Giraffa camelopardalis*) away from the riverfront (Vanderwalle 2000), thereby alleviating pressure on the riverine vegetation allowing regeneration and growth, and thus accounting for the taller and greener grass stands in which puku and lechwe fed during the HWS.

Selection of short grass areas may also have served as a predator avoidance tactic. By foraging in short grass areas puku and lechwe would have been able to see predators approaching at a distance, and then move to safety.

Faecal N and P levels are correlated to N and P in the diet consumed by an animal (Moir 1960; Belonje 1980; Grant *et al*., 1995). Faecal nitrogen has also been shown to reflect forage digestibility (Moir 1960; Holechek *et al*., 1982). These correlations have been shown to be improved if faecal N and P are considered together, because their excretion is linked (Moir 1966; Grant 1989; Grant *et al*., 1995), and if the season and habitat type are defined (Grant 1989; Grant *et al*., 1995). Rumen fermentation is said to be disrupted if faecal N concentrations are not at least 1.1% - 1.2% (Grant *et al*., 1995). Concentrations of faecal P are considered deficient if below 0.2 % dry mass (DM) (Stowe, 2003). Faecal values presented by Grant *et al*. (1995) and Stowe (2003) were calculated from the observations on large ungulates such as buffalo, zebra, and wildebeest and may therefore not be accurately applicable to smaller bodied ungulates such as puku and lechwe. Faecal nutrient values obtained from sheep, a similarly sized ruminant to puku and lechwe, showed faecal nitrogen values

to be sufficient when within the range of 1.5% - 4.64 % and faecal phosphorus values to be sufficient when in the range 0.82% - 1.16% DM (Jones, 1971). The sheep used for the study by Jones (1971) were domestic livestock, and were receiving high quality forage to encourage growth, rather than mere survival. We can therefore expect levels of faecal N and P slightly lower than those reported by Jones (1971), to be sufficient to maintain condition in wild populations of puku and lechwe in Chobe.

Faecal N values obtained for puku and lechwe remained above the critical threshold, recommended by Grant *et al.* (1995), across both seasons. When compared to the critical limits defined by Jones (1971), faecal nitrogen values of puku and lechwe lay at the low end of the scale. Using the value of 0.2% DM to represent the critical basal limit for phosphorus (Grant *et al*. 1995; Stowe 2003), suggested neither puku nor lechwe were deficient of phosphorus at any period of the year. However, when compared to the critical limit suggested by Jones (1971), both puku and lechwe appeared to be deficient of phosphorus for the full extent of the annual cycle. As mentioned, the comparison of faecal N and P values of puku and lechwe to those of domestic sheep may be misleading. Puku and lechwe populations along the Chobe River have persisted thus far, indicating that faecal N levels of >1.5%DM and faecal P levels of >0.25%DM are more than sufficient to ensure survival of the populations. Even though the results presented here suggest both puku and lechwe obtain sufficient N and P to ensure survival, it is less clear what the potential influences on reproduction are. Inadequate intake of nitrogen or phosphorus may lead to irregular estrus, low contraception, fetal reabsorbtion, or weak offspring, whereas an excessive intake of nitrogen may lead to low contraception rate (Bearden & Fuquay 1992). Further study is therefore needed to distinguish critical thresholds of N & P intake for puku and lechwe.

The only significant seasonal variation in faecal N and P values was for puku faecal P. The level of puku faecal P increased from the LWS to the HWS. This result was contrary to the null hypotheses that a critical period in nutrition would be faced

during the HWS. Rees (1978) showed P to be deficient in floodplain soils along the Kafue River, Zambia, and Stowe (2003) showed P deficiencies in floodplain grasses of the Okavango Delta, Botswana. It is therefore possible that the floodplains along the Chobe River are also P deficient, and the increase in puku faecal P is a direct result of puku foraging within shrubland habitats with higher soil P concentrations. A study analyzing P concentrations in soil samples taken at various intervals along the catena next to the Chobe River would provide valuable insight into the relationship between puku faecal P in relation to the habitat occupied.

A decline in the availability of preferred grass species due to inundation of the floodplains may have been counteracted by the influence of rainfall. Along the Chobe River system, the HWS generally coincides with the rainy season. The effect of reduced availability of preferred grass species within the floodplains may therefore have been buffered by an increase in availability of green, nutritious grass within grassland and shrubland habitats. The flush of green, nutritious grass during the HWS appeared to be sufficient to maintain nutrient levels in puku and lechwe. Greater perspective on the condition of puku along the Chobe River may be gained from comparison to other puku populations. Comparisons of faecal N and P from Chobe puku populations to the thriving puku populations of Luanga (Zambia) may give a better indication of the nutritional condition of puku along the Chobe riverfront, and allow for better understanding of critical nutrient levels specific to puku.

The limitation of this study was the basis for the determination of the diets of puku and lechwe. All dietary proportions in this study were determined through the use of two methods. Direct observation estimated the proportion of any particular grass species in the diet by examining the number of grass tufts that were fed upon. The notable shortfall of this method was that with populations of wild herbivores, there is no way of quantifying the bite size on a particular grass tuft. A grazed grass tuft that has been bitten three times will be recorded the same way as a grass tuft that has only

one bite from it. In an attempt to accurately determine the proportions of grass species in the diets of puku and lechwe, microhistological analysis was used to validate the results from direct observation. Accuracy of microhistological faecal analysis may however, be affected by the extent of digestion of plant epidermis as it passes through the alimentary tract of a ruminant (Stewart, 1967; Slater & Jones, 1971; McInnes *et. al.* 1983; in Leslie *et. al.* 1983). More readily digested grasses are underestimated in the faeces while less readily digested grasses are overestimated in the faeces (Brand, 1978). Microhistological faecal analyses may also be subject to bias arising from sample preparation in the laboratory (Vavra & Holechek 1980). Firstly, sample preparation such as the grinding of faecal material can destroy epidermal fragments, thereby invalidating the assumption that grinding the material to the same size is necessary to obtain the 1:1 ratio needed of relative density to percent weight. Secondly, certain grass species may undergo greater in vitro destruction than other species. Predetermined season-specific, grass species-specific, and animal species-specific correction factors may have improved dietary estimates of grass species in the diets of puku and lechwe (Pulliam & Nelson, 1979).

When using both direct observation and faecal analyses in conjunction with one another, as in this study, it must also be remembered that variation in results may have been a consequence of differences in the sampling periods of the methods (Sanders *et al*., 1980). Direct observation took place between the hours of 06h00 and 11h00, and therefore made no account of the afternoon or nocturnal feeding of puku and lechwe. Grasses fed upon during these periods would thus not be accounted for by direct observation. Microhistological faecal analyses had the advantage of estimating the animals' diet for up to a 6-day period, as this is how long it may take ingesta to pass through the digestive tract (Church 1969; Sanders *et al*., 1980).

Differential digestibility of grass species (Stewart, 1967; Slater & Jones, 1971; McInnes *et. al.* 1983; in Leslie *et. al.* 1983) may account for the differential results obtained between faecal analyses and direct observation for *C. dactylon, D. aegyptium, Eragrostis spp.,* and *P. mauritianus* in the diet of puku. *Cynodon*

dactylon appeared to be digested to a greater degree than other grass species in the diet of lechwe. Conversely, the main limitation of direct observation, of not being able to quantify bite size, was clearly evident for *A. adscensionis* and *B. eruciformis,* both of which were underestimated in the diet of puku, in both seasons. Differences between the methods of observation were less distinct for grasses in the diet of lechwe. Although specific seasonal differences in the estimates of dietary proportions of grasses in the diet of lechwe did exist, only *C. dactylon* was consistently underestimated through faecal analyses compared to direct observation.

In light of the obvious biases in both methods, the critical question is, which method, direct observation or microhistological faecal analyses, provides estimates that are closer to the true dietary contributions of grasses in the diets of puku and lechwe? Results from this study suggest that either method may have been suitable for determining the diet of lechwe. Both direct observation and faecal analyses provided similar results for the major components in the diet of lechwe. Results for puku were more varied between methods. In cases such as here with puku, it may be viable for future studies to calculate an 'average method proportion', where the contribution to the diet of a particular grass species is calculated as (proportion from direct observation + proportion from faecal analyses)/2. The resulting figure then represents the average contribution of that grass species between the two methods. It may be argued that this value is an average of an average, and thus not a true mean estimate of the contribution of that grass species to the diet. The value however, still holds biological significance in that it serves to balance conflicting results from both methods. A further advantage of this calculation is that grasses with similar values between the two methods are not significantly altered and will still give estimates similar to those from direct observation and faecal analyses.

2.7 Key results

- The diets of puku and lechwe along the Chobe River were composed entirely of grass species.
- Levels of dietary overlap between puku and lechwe were 84.1% and 89.9% during the LWS and HWS respectively.
- Seasonal acceptance of grass species by puku was most strongly dictated by the height of the grass sward, with shorter grasses generally attaining higher acceptance values. Lechwe were only selective towards grass height during the HWS. Grass greenness did not appear to have an influence over acceptance of grass species.
- Puku and lechwe could not be differentiated in features important to the selection of foraging sites.
- Neither puku nor lechwe were found to be deficient in N or P during the LWS or the HWS.

CHAPTER 3

COMPARATIVE HABITAT SELECTION OF PUKU AND LECHWE ALONG THE CHOBE RIVER IN NORTHERN BOTSWANA

3.1 Introduction

Ecological research is connected by an underlying desire to understand the influences that dictate the distribution and abundance of species (McLoughlin *et al*. 2009). By describing the distribution and abundance of animals we are able to explore the interactions between these animals and their environment (McLoughlin *et al*., 2009) as well as interactions between animal species. The determination of which resources are selected with greater frequency than others provides vital information about how animals meet their needs for survival (Manly *et al*. 2002). An understanding of the availability of resources and habitats to endangered animal species in particular, is critical in conservation efforts.

Disproportionate habitat selection is often assumed to a function of fitness maximization by an animal (Rosenzweig 1981; Morris 2003). Factors that strongly influence herbivore habitat selection include predation (Mech 1977), forage distribution (Fryxell *et al*. 2004) and competition (Fretwell & Lucas 1970). The most direct effect of predation is the reduction of prey numbers by predators (Valeix *et al.* 2009). Indirect effects of predation, such as alteration of prey behaviour may also be important considerations in habitat selection studies. Examples of prey behavioral modification include the selection of specific habitat structure (Wirsing *et al.* 2007), spatial redistribution (Ripple & Beschta 2004), spatial and temporal changes in activity patterns (Fenn & Macdonald 1995), and increased vigilance and reduced foraging time (Abramsky *et al*. 2002). The impact of mammalian predators on their prey may have important implications in the management of some species (Mills & Shenk, 1992). Elk in Yellowstone National Park were shown to adapt their habitat selection in accordance with avoidance of wolves (Mao *et al.* 2005). Elk avoided

wolves by selecting areas with higher elevations, less open habitat, and steeper slopes (Mao *et al.* 2005). Lechwe have reported to flee though shallow water to avoid predators (Mills & Hes, 1997). Breeding behaviour of Ugandan kob appears to be influenced by the need to avoid predators, with leks (breeding areas) generally being selected in areas of particularly low cover thereby allowing for early predator detection (Gosling, 1986; Gosling & Petrie, 1990). Selection of habitats therefore appears to arise from the need to minimize predation risk while still meeting nutritional requirements (Gilliam & Fraser, 1987; Pulliam, 1989).

Large herbivore species are influenced by elevated nutrient concentrations in the forage upon which they feed (Owen-Smith & Novellie, 1982; Bryant *et al*., 1989; Ben-Shahar & MacDonald, 2002). Feeding patterns and differential distribution of herbivore species may be explained by localized differences in soil factors and nutrient levels (McNaughton, 1990; Ben-Shahar & Coe, 1992; Ben-Shahar & MacDonald, 2002). Net primary productivity of plant species depends critically on the concentrations of essential mineral nutrients, such as nitrogen and phosphorus, in the soil (Townsend *et al*., 2000). Environments containing high levels of nitrogen and phosphorus in the soil may thus be expected to have increased levels of plant growth and/or plant species containing elevated levels of nutrients. Frank *et al*. (1998) showed plant concentrations of boron, calcium, cobalt, copper, iron, magnesium, nitrogen, sodium, and phosphorus were significantly related to soil concentrations. Westoby (1974) suggested that ungulates optimize their foraging behaviour to obtain an optimal mix of nutrients from a fixed total intake of food. Accordingly, ungulates should attempt to maximize nutrient intake by foraging within habitats with a high proportion of nutritious plant species. Bison (*Bison bison*), elk (*Cervus elaphus*), pronghorn (*Antilocarpa americana*), wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) have all been shown to seasonally migrate between eutrophic and dystrophic habitats along nutrient gradients (Frank *et al*., 1998). Seasonal migrations thus highlight the high spatiotemporal

variation in forage and the close association between the spatial pattern of high quality forage and ungulate distribution within an ecosystem.

Spatiotemporal variation in forage within African savanna ecosystems is determined primarily by patterns of precipitation across those ecosystems. Spatially, both abundance and quality of forage vary at different scales of ecological resolution (Senft *et al.,* 1987). Regionally, the largest scale can extend over hundreds of square kilometers incorporating differing landscapes and vegetative communities. Forage quality and quantity within each of these communities is determined through soil nutrients and water availability (Bell, 1971, 1982, 1984; Vanderwalle, Chapter 3, 2000). At finer scales, local variations in soil nutrient levels and soil water availability determine the distribution and selection of forage by animals, and form the basis for ecological separation of habitat types via specific vegetation classifications growing in specific soil types. Wildebeest and zebra in the Serengeti migrate against a gradient of mean annual rainfall from infertile grasslands in the dry season to fertile grasslands during the wet season (Grzimek & Grzimek, 1960; Talbot & Talbot, 1963; McNaughton, 1979; Frank *et al.,* 1998). Similarly, seasonal migrations between distinct habitat types (grasslands and savanna) are reported in zebra and wildebeest herds in northern Botswana (Vanderwalle, Chapter 3, 2000).

Seasonal migrations of certain species may occur due to processes that are functionally similar to migrations fuelled by rainfall, but have radically different environmental factors. Ungulates in Yellowstone National Park migrate along an elevation gradient, between low-elevation winter habitats and higher elevation summer habitats (Frank *et al.,* 1998). Herbivores considered as floodplain species, such as puku and lechwe, are often strongly influenced by the flood regime of the river system along which they inhabit. As Williamson (1990) reports, lechwe in the Linyanti Swamps are forced to retreat to upland areas as the floodwaters of the wet season arrive. During the dry season, animals are then able to return to low lying floodplain areas. For example, during the high water season, lechwe in the Kafue

Flats region of Zambia are confined to a narrow fringe of habitat, within 0.5km of water, along the termitaria zone or even woodlands adjacent to inundated floodplains, but avoid dense bush (Robinette & Child 1964, De Vos & Dowsett 1966). During low water periods lechwe in the Kafue Flats are observed to follow the receding waters and make use of the newly exposed floodplain.

Sheppe & Osbourne (1971) suggest the high water season is the most critical for lechwe and other floodplain dwelling ungulates, since they are crowded into a narrow zone around the edge of the inundated floodplains or into small areas of exposed high ground within the floodplain. As the animals crowd into remaining habitats, competition for resources is expected to be high. Increased levels of competition for resources during certain periods may be critical to individuals leading to a dependence on key resources. Knowledge of which habitats are being utilized by animal species during critical periods is therefore an essential facet in wildlife management and conservation.

Understanding the underlying habitat selection processes of animals, endangered or rare animals in particular, is critical in the formation and application of successful management practices. The distribution of puku in Botswana is highly localized and restricted along the banks of the lower reaches of the Chobe River within the Chobe National Park. Notably, the congeneric species lechwe (*Kobus leche*) both overlaps and exceeds the distribution of puku within Botswana. A comprehensive description of the puku and lechwe populations within the Chobe National Park, and elsewhere, is given in **Sections 1.1**, **1.2**, and **1.3** of **Chapter 1**.

Previous studies conducted on puku and lechwe (Rees, 1978[a, b]; Williamson, 1990; Dipotso & Skarpe, 2006) have given strong indication that both species occupy similar habitats. Describing the habitat selection of these sympatric species thus becomes an important factor in the determination of ecological separation as well as explaining the context of intraspecific competition (Sale 1974).

The low population size and extremely localized and isolated distribution of puku within southern Africa highlight the urgent need for study and conservation of this species. In this chapter I investigated possible changes in habitat selection and range size of puku and lechwe over a one-year period. I hoped to highlight any significant differences or similarities in habitat selection between the two species that may indicate possible reasons for the limited distribution and low population size of puku, in Botswana, compared with the more widespread and abundant lechwe.

The aim of this chapter was to investigate the seasonal habitat selection of puku and lechwe and to offer some insight into the mechanisms driving habitat selection by these species. This was achieved through the following objectives:

1. Establishing and defining habitats selected by puku and lechwe.
2. Investigating how habitat selection changes in relation to the seasons.
3. Analyzing any differences between habitat selection of puku and lechwe in each of the seasons.
4. Determining the effects of vegetative physical characteristics and topographical features on habitat selection.
5. Estimating and comparing the population range size of puku and lechwe in each of the seasons.

The objectives listed above, led to the following hypotheses:

1. Areas that were recently exposed by receding water or were in shallow swamp would be selected with greater frequency by lechwe compared to puku. Habitats in dry, low lying areas of floodplains would be selected with greater frequency by puku compared to lechwe.
2. Habitat selection by puku and lechwe would remain constant and not change significantly between seasons, throughout the year.

3. To avoid predators, puku and lechwe would select against habitats with high levels of visual obstruction. Lechwe would select habitats at close proximity to escape terrain, such as water, to escape predation.
4. The size of puku and lechwe population ranges would be the similar between species, and not vary significantly between seasons.

3.2 Materials and methods

3.2.1 The study area

A detailed description of the study area is given in **Section 1.8** of **Chapter 1**.

3.2.2 Data collection

This study followed a *sampling protocol A,* with a *design I* format (Manly *et al.* 2002), and due to the lack of individually identifiable animals habitat selection patterns were described at the population level. Habitat use by puku and lechwe was assessed via measurements made in sampling units which were considered to be either used or available. In this study, used and available units were randomly sampled with measurements being made at the level of the population. Units were classified as being either 'used' or 'available' as opposed to 'unused' because it was not possible to determine accurately if a particular habitat type had been used previously, or would be used in the future.

3.2.2.1 Sampling used habitat sites

Habitat selection by puku and lechwe was centered on foraging sites. I chose to base the habitat analyses around the foraging sites of puku and lechwe as these can be accurately quantified as being 'used'. Other methods such as habitat analyses based

on the locations of animal tracks (see Neu *et al.* 1974) may be misleading as difficulty may arise in differentiating between which habitats have been used explicitly for biologically important functions (such as feeding or sleeping) and which habitats have merely been utilized as transit routes.

The general study area was divided into five intensive study sites based on the locations of puku and lechwe. Each intensive study area extended northwards from the 'top road', along the crest of the sand ridge, to the main channel of the Chobe River (**Figure 6**). Each of the intensive study areas were subdivided into four roughly equal sized subunits. Each of the intensive study sites were then sampled on consecutive days beginning in a randomly selected subunit and progressing consecutively through each of the remaining subunits (**Figure 6**). Observation spanned a period of one year, beginning 1 July 2007 and ending 31 June 2008.

On each day of observation foraging puku and lechwe were located with the use of an Elite 80 mm, 10 – 60 times magnification spotting scope. A Bushnell Yardage Pro 400 laser range finder was then used to calculate the exact distance from the observer to the foraging location. At the location of the herd, a foraging site was determined by the presence of spoor, droppings, and freshly cropped grass. A foraging site was defined as the entire area where the animals were feeding for at least 15 minutes (Magome *et al.,* 2008). Foraging sites were considered independent of one another when separated by a minimum distance of 200 meters. At each foraging site, a feeding site was identified by freshly cropped grass. To avoid the risk of puku and lechwe foraging sites being altered by other animals, these areas were sampled immediately after the focal species had ceased to forage or moved away. All sampling took place during the morning between the hours of 06h00 and 11h00 while puku and lechwe were still actively feeding. By observing feeding behavior for a period of 15min prior to sampling, and by using a range finder to accurately determine the exact foraging location of puku and lechwe, I believe that the potential

for foraging sites to have been altered by nocturnal foraging of non-target species to be inconsequential.

To determine habitat use by puku and lechwe certain habitat variables were measured and recorded. Five variables were measured within a 25 m radius of the centre of the foraging site and included; habitat type, predominant vegetation class, percentage shrub cover, percentage tree cover, and the level of visual obstruction.

Habitats within the study area were defined based on the predominant vegetative structures and/or physical features of the immediate (25 m radius) area of occupation. The following 8 habitat types were identified; **shallow swamp** – defined as an area containing aquatic vegetation with the water level being less than 1m deep; **interface zone** - the area of moist soil between dry land and water; **low-lying floodplain** – floodplains that experience inundation for a period of 3-8 months; **high-lying floodplain** – floodplains that experience inundation for a period of less than 3 months; **grasslands** – areas not inundated at any period during the year, and predominated by grass species with less than 5% shrub or tree cover; **termitaria** – areas centered around termite mounds; **shrublands** – areas predominated by woody vegetation ≤5 m in height; **woodlands** – areas predominated by woody vegetation >5 m in height.

The predominant vegetation was classified as one of 12 broad-scale vegetative categories; annual-hydrophytic, annual-helophytic, annual-xerophytic, perennial-hydrophytic, perennial-helophytic, perennial-xerophytic, annual or perennial, *Combretum species, Croton megalaboris, Capparis tomentosa, Erythroxylum zambesiacum, Baikea plurijuga.* At each of the sampling sites (available or used) each of the respective vegetation classes were then recorded as being either absent from that site, or present at that site. The percentage basal cover of shrubs (≤5 m in height) and trees (>5 m in height) within the 25 m radius of the foraging site was estimated visually. Visual obstruction was assessed with the use of a Robal pole.

The Robal pole was subdivided into 10 cm segments. The Robal pole was then placed 25m away from the centre of the foraging site, in each of the cardinal directions. The sighting pole was set to a height of 1m, which is the average head height of puku and lechwe, so as to give a more biologically meaningful estimation of the level of visual obstruction as seen by the animal. Looking from the sighting pole in the center of the foraging site the number of visible 10 cm segments was recorded and subtracted from 1 m to give the level of visual obstruction e.g. if 3 segments were clearly visible then the level of visual obstruction was 70%. The four values from the cardinal points were averaged to give a single estimate of the visual obstruction at that foraging site.

Three habitat variables were evaluated through the use of quadrats placed within the identified foraging site. A central quadrat (0.7 m x 0.7 m) was placed over an area of freshly cropped grass. A further eight quadrats were then placed within the foraging site; two in each of the cardinal directions around the first quadrat (**Figure 9**). Each quadrat was placed 2 m apart from the other quadrats. Within each of the quadrats the following variables were recorded – percentage grass cover, grass greenness, grass height. The percentage grass cover was estimated visually as the basal grass cover within each quadrat. Grass greenness was estimated visually as the proportion of green leaves of the grass swards within each quadrat. Grass height was calculated from measurements from the ground to the tip of the highest leaf of the predominant grass species. The values obtained from all nine quadrats were then averaged to give a single value estimate for each variable for that foraging site.

A final variable to be recorded was the distance to water. With the use of a range finder, the distance to the nearest point of the Chobe River from the centre quadrat was recorded. All the variables recorded at foraging sites, and their associated scales of measurement, are presented in **Table 1**.

3.2.2.2 Sampling available habitat sites

As indicated in the literature (Child 1968, Child & von Richter 1969, Spinage 1986, Mills & Hes 1997, Dipotso & Skarpe 2006), and based on my observations during a preliminary study, puku and lechwe fed almost exclusively on floodplains and nutrient rich grasslands. However, I postulated that during periods of high water much of the available floodplains would become inundated thus forcing the puku and lechwe into the shrubland and woodland areas along the escarpment.

During low water periods when puku and lechwe concentrated feeding on floodplains, the choice of habitats within these areas had little to do with the conditions in the shrubland and woodland areas. During high water periods, much of the floodplain habitats became inundated or inaccessible to puku and lechwe and as a result both species were forced into grassland, shrubland and woodland areas. The choice of foraging sites within shrubland and woodland habitats during high water periods therefore had little to do with conditions in habitats on the unavailable floodplains. Estimation of available habitat was therefore conducted seasonally based on the water levels of the Chobe River (**see Figure 4**).

3.2.2.2.1 Low water season

Habitat availability during the LWS was estimated through the use of line transects walked through the floodplains in each of the intensive study sites. In the Watercart, Puku Flats, and Lechwe Flats study sites a park road extended along the southern edge of the floodplains. Beginning at the western edge of each of the intensive study sites, and moving east, line transects were walked from the road, to the river, in a north-south and south-north direction. No roads existed within the Kabulabula and Sedudu Island study sites, therefore transects were walked from a hypothetical road extending along the southern edge of the study sites. Transect lines were spaced 200m apart. Along each transect line, sampling points were spaced every 200m; the

number of sampling points per transect depended on the length of the transect. Due to the short distance from the road to the river in the Watercart study site sampling points were taken every 100m as opposed to every 200m. Sampling conducted at points every 200m would not have given an accurate representation of the available habitats within the Watercart study site. At each sampling point along the transect lines the same habitat variables as those recorded at puku and lechwe foraging sites were documented using the same methods as those described in section 3.3.1.1.

During the first month of transect sampling the GPS location of each sampling point along the transect lines were recorded to ensure accurate repeatability of measurements. Transects were sampled during the last week of every month for the duration of the study. This gave an indication of the seasonal variability in phenological characteristics and the availability of the vegetation within each available habitat type in accordance with the seasonal rainfall and flood levels. The number, position and length of the transects walked in each study site was dependent on the position of impassable water and the presence of potentially dangerous animals such as buffalo (*Syncerus caffer*), elephant (*Loxodonta africana*) and lion (*Panthera leo*). In total, 185 points were sampled along 37 transects during each month of the LWS (**Figure 24**).

3.2.2.2.2 High water season

With the onset of the rains and the gradual rise of the floodwaters much of the available floodplain habitats sampled during the low water season started to become inundated, resulting in a decline in the number of available sampling points along the initial 37 transects. The rising floods had the effect of pushing puku and lechwe populations off the floodplains and into the grassland, shrubland and woodland habitats. To ensure accuracy and reliability in the estimation of the seasonal availability of habitats, it became necessary to conduct transects within the upland areas (in addition to those transects still accessible on the floodplains). These

additional transects were only conducted during the HWS because as mentioned previously, shrubland and woodland habitats were not seen to be utilized by puku and lechwe during the LWS.

The additional transects were sampled within the shrubland and woodland areas immediately adjacent to the Watercart and Puku Flats floodplains. Transects were conducted along the park roads traveling in a westerly direction parallel to the Chobe River. It is acknowledged that using the park roads as transect lines may be associated with a certain level of bias, however, conducting transects in the upland areas away from the road was not feasible due to the low visibility coupled to high concentrations of buffalo, elephant, and lion. The park roads were sandy tracks that were not subjected to high traffic levels. Sampling points were taken at 200m intervals with the same variables being recorded as in section 3.2.1. Each sampling point was located at a perpendicular distance of 50 m from the southern edge of the road. A total of 27 additional points were sampled in the HWS along two roads traversing the lengths of the Watercart and Puku Flats study sites (**Figure 24**).

At the height of the floods Lechwe Flats, Watercart and Sedudu Island were completely inundated by water and were unavailable to both puku and lechwe. Kabulabula, although not completely inundated, became inaccessible by vehicle or on foot. Access to Kabulabula by boat was not feasible due to its distance from Kasane (the base for the study). Puku Flats also became inaccessible by vehicle or on foot but limited access was available by boat. However, due to low visibility and shallow swamp, working conditions in this site were risky and dangerous to the observer and thus the numbers of observations in this site during the HWS were lower.

During high water periods, the Kabulabula floodplains were in fact cut off from the escarpment areas by a wide, deep water channel. Puku and lechwe in this area were in effect, isolated on an ‘island’. The floodplain vegetation on the ‘island’ was vastly different to that encountered within the escarpment areas and thus the escarpment vegetation during the high water season had no bearing on the vegetation available to

puku and lechwe within the Kabulabula study site. Both Kabulabula and Puku Flats were however still accessible and utilized by puku and lechwe during the high water seasons. Results pertaining to habitat use during the HWS were biased towards upland habitats due to accessibility restrictions of the observer.

3.2.3 Data analyses

3.2.3.1 Logistic regression

Measurements obtained from the used and available sampling units were entered into logistic regression analyses. Regression models have become an integral component of data analyses concerned with describing the relationship between a response variable and any number of explanatory variables (Hosmer & Lemeshow, 2000). The goal of the logistic regression model is to distinguish the best fitting and most parsimonious model to describe the relationship between an outcome variable and a set of independent variables. In the case of this study the outcome variable was binary i.e. it took on one of two possible values, used or available (Hosmer & Lemeshow, 2000).

All available resources sampled during the last week of every month (as described above) were averaged per season for each sampling point. Seasonal mean values for each of the continuous variables recorded (see section 3.3.1) were calculated by summing the values and dividing the total by the number of months that that point was available in each season. Classifying habitats throughout a season became an arduous task due to the variable nature of floodplain environments. Habitats defined within floodplains may constantly change and be redefined monthly throughout the annual cycle of inundation and recession of floodwaters **(Figure 25)**.

Habitats classified as ‘low-lying floodplains’ during the LWS could be reclassified as being either ‘interface zone’ or ‘shallow swamp’ during the HWS. To gain accurate

assessments of the proportions of available habitats within floodplains it was necessary to take into account the variable nature of floodplains by sampling and estimating availability in each season.

Each of the defined seasons spanned a period of 6 months. If, for example, 'shallow swamp' was recorded as the habitat class at a given sampling point for 4 months and recorded as 'low-lying floodplain' for 2 months, then the seasonal habitat class was classified as 'shallow swamp' – the predominant of the two habitat classes in that season.

In **Figure 4**, it can be seen that the flood waters rose quickly during the first 3 months of the HWS and then gradually declined over the course of the following season. I therefore made the assumption that habitat classes defined as 'shallow swamp' or 'interface zone' would exist for the greater part of a season than would 'low lying floodplain' or 'high lying floodplain'. Therefore, if a habitat class was defined as 'low lying floodplain' for 3 months and 'shallow swamp' for 3 months, then the habitat class was defined as 'shallow swamp' due to the gradual tapering off of the water levels. If a sampling point was classified as being 'shallow swamp' for 3 months and 'interface zone' for 3 months, then that point was regarded as being 'shallow swamp' for the season. Again, the reason for this being that due to the gradual decline of the water level, that sampling point had a greater chance of being inundated (and therefore classified as shallow swamp) for a longer period during that season, than it did of being exposed and classified as 'interface zone'.

The variables were entered in to the logistic models as being either continuous or categorical. Habitat type was entered as a categorical variable with eight classes coded as follows; shallow swamp = 0, interface zone = 1, low lying floodplain = 2, high lying floodplain = 3, grasslands = 4, shrublands = 5, woodlands = 6, and termitaria = 7. Shallow swamp was set as the reference category. Results pertaining to use of the remaining habitat types were thus compared to the odds of use of shallow swamp. Predominant vegetation classifications (e.g., annual–hydrophytic,

annual–helophytic, annual–xerophytic, etc...) were entered into the analysis as dichotomous dummy variables, coded as 0 if the variable characteristic was absent and 1 if the variable characteristic was present (e.g., for annual-hydrophytic, all sampling points not located in annual-hydrophytic vegetation were coded as 0 and all points within annual-hydrophytic vegetation were coded as 1). The remaining variables; distance to water, grass height, grass greenness, grass cover, shrub cover, tree cover, and visual obstruction, were entered as continuous variables. Each of the continuous variables was tested for normality prior to analyses.

The dependent variable was given a value of 0 if a sampled site was available and 1 if the sampled site was used by either puku or lechwe. I therefore had a sample of available resource units and a sample of used resource units. The logistic regression model was used to examine how the probability of use of a site by puku and lechwe was related to the habitat variables that were collected (Manly *et al.* 2002).

In total there were 20 candidate variables (7 continuous and 13 categorical) that were available for use in each of the seasons to determine the probability of use of a site. Before conducting logistic regression I conducted preliminary data exploration by using and adapting the methods outlined by Hosmer & Lemeshow (2000) and Bombay *et al.* (2003). Preliminary data analyses helped to reduce the number of variables included in the respective models in each season. I used a 5 step process for analyses of each model in each season.

Step 1: Variables with seasonal frequencies of less than 5 were dropped from the analyses. Variables with frequencies of less than 5 in a season could not be accurately tested for normality and were excluded from further analyses in the model.

Step 2: A uni-variable logistic regression was performed on each of the remaining variables. Any variable that had a significance value of $P \geq 0.250$ was excluded from further analyses unless knowledge of puku or lechwe biology precluded exclusion of

that variable. Using the 0.250 level of significance was based on the recommendations of Bendel & Afifi (1977) and Mickey & Greenland (1989) in Hosmer & Lemeshow (2000). A more traditional level of 0.05 may have excluded variables that were known to be important. Higher levels of significance ran the risk of including variables that had questionable importance at the model building stage.

Step 3: Pearson's correlation coefficient was used to check for any bivariate correlations between remaining variables. If any given pair of variables attained a correlation coefficient of > 0.8, one of the variables was dropped from the analyses. The variable that was thought to provide the greatest biological value was maintained in the model. If it was thought that dropping a variable would result in a loss of biological information then both variables were kept in the model.

Step 4: A forward stepwise logistic regression was performed with all the remaining variables included in the analyses. Limits for entry and removal of variables into the logistic model were set at 0.10 and 0.15 (Hosmer & Lemeshow, 2000). The results of research (Bendel & Afifi, 1977; Costanza & Afifi, 1979; Lee & Koval, 1997; Hosmer & Lemeshow, 2000) have shown that an entry level of 0.05 to be too stringent, often excluding important variables from the model.

Forward stepwise logistic regression was used in all models. This method was chosen because it does not assume linearity of relationship between the independent and dependent variables, is robust even with departures from normality in the variables, and does not assume homoscedasticity (Garson, 2009). The model does however require independence of observations and that the independent variables are linearly related to the logit of the dependent (Garson, 2009). In forward stepwise regression, starting with the constant-only model, variables are added one step at a time based on their 'Score' statistic (variables with higher scores being added first) until a cut-off level is reached. Variables are no longer added to the model once all the variables not in the model have a significance of >0.10. Variables were added to the model if the score statistic was ≤0.10 and removed from the model if the

likelihood ratio was >0.15. The relatively wide inclusion and exclusion limits ensured that variables with marginal significance values (e.g. $P = 0.056$ at the 5% significance level) were retained in the model. Subsequently, it was then decided if the marginal variables in the model were biologically significant even though not technically statistically significant. If a variable was considered to be biologically significant it was retained in the model. Results presented for dichotomous categorical variables predict the odds for one category in reference to the other. In this study the reference category was set to the first category i.e. the 0 = 'available' category. Thus, the parameter estimate refers to the change in the log odds when the dummy variable is 1 (use), compared to the reference category (available) equaling 0 i.e. what is predicted by the model are the odds for use of a foraging site.

Step 5: The final step in the model building process was to assess the fit of the model and interpret the results. Interpretation of the results from the forward stepwise logistic regression was done by examining the odds ratio of each variable. The odds ratio for a given independent variable represents the factor by which the likelihood of the outcome (i.e., probability of use) to occur for a one unit change in the independent variable. Overall model fit was assessed using 3 methods: **i**) A Hosmer & Lemeshow chi-squared test was used to determine if the observed values in a model differed significantly from the model-predicted values. If the Hosmer & Lemeshow goodness-of-fit statistic is greater than 0.05, then there is no difference between observed and model-predicted values. The Hosmer & Lemeshow chi-square test was used as the main test to assess overall fit of a given logistic regression model. This test gave an indication of whether or not the model's estimates fit the data at an acceptable level. **ii**) A Pearson chi-squared test was used to ascertain if a model containing the predictor variables was significantly different to the model containing the intercept only. The chi-squared test revealed if any of the predictor variables in the model had a significant relationship to the response variable. The Pearson chi-square test was conducted at the 0.05 significance level. **iii**) Classification tables - The specificity and sensitivity of the model was assessed to determine if the model

was capable of predicting whether a site was used or available better than by chance alone. Classification tables were not used as a direct measure of goodness-of-fit, but rather to supplement the results of the Pearson and Hosmer & Lemeshow chi-square tests. A cut-point value of 0.5 was used for classification. Specificity indicated the percentage correct classification of available sites, and sensitivity of the model indicated the correct classification of the used sites. All analyses were performed using SPSS version 10.0 (SPSS Inc., Chicago, Illinois, U.S.A) and tests of model coefficients were conducted at the 0.10 significance level. The specific variables entered into each model in each season, and the number of models produced by the forward stepwise logistic regression procedure, are listed in **Table 2**.

3.2.3.2 Comparative habitat use of puku and lechwe

ANOVA was performed on each of the continuous variables to assess the magnitude of the difference in the habitat variables between puku, lechwe and availability. Individual replicates in ANOVA analyses were the foraging sites sampled in each season. The independent variables in each analysis were species and season. Separate ANOVA analyses were performed using each of the continuous variables as the dependent variable. The models were; species x season x grass height, etc. All analyses were conducted using SPSS version 10.0 (SPSS Inc., Chicago, Illinois, U.S.A) and tests were conducted at the 0.05 significance level, unless otherwise stated.

3.2.3.3 Used population range estimation

Since this study focused on the populations of puku and lechwe, thus range estimation was at the level of the population i.e. not the home range which specifically refers to the range of an individual. Estimates of population range in this section are further defined as being the **used** population range because they refer specifically to areas utilized for foraging. Estimates of population range

(incorporating areas used for travel and bedding) may be expected to be higher than the estimates reported here for the used population range. Estimates of the seasonal used population ranges of puku and lechwe were determined from global positioning system (GPS) locations taken at each of the foraging sites using a Garmin Foretrex (Garmin, Kansas City, USA) hand held GPS unit. Estimations of seasonal population ranges for puku and lechwe were calculated using 100% minimum convex polygons (MCP's) in the Hawth's Tools (www.spatialecology.com) extension for ArcMap (version 9.0, ESRI, Redlands, California). A separate MCP was created for each unique study site. The MCP areas from each of the study sites were totaled to give an overall estimate of the used population range. By creating a separate MCP for each of the study sites, areas not used for foraging by puku and lechwe which lay between study sites, were excluded from the estimation of the used population range. A disadvantage of using MCPs is that MCPs have been shown to be highly sensitive to sample size (Laver, 2005) with the size of the range increasing with each additional sampling point being added to the analyses. A further disadvantage of 100% MCPs is the inability of the polygon to objectively treat outliers (Seaman *et al.* 1999). Seasonal population ranges were calculated for both puku and lechwe in each of the seasons and compared descriptively to give an indication of the effect of seasonal inundation of the floodplains on used population range size.

3.3 Results

3.3.1 Seasonal Habitat Selection

Low water season. The model best suited (Model 4, Hosmer & Lemeshow χ^2 = 7.88, *D.F.* = 8, *P* = 0.445; Pearson χ^2 = 16.99, *D.F.* = 5, *P* = 0.005, **Table 3**) to predicting habitat use by puku during the LWS included habitat type, grass cover, grass height, and grass greenness. Specificity (89%) and sensitivity (44%) produced an overall model predictive accuracy of 73%. The interface zone was 13 times (Odds ratio = 13.28, *90% CI* = 1.87 to 94.20, *P* = 0.030) more likely to be utilized for

foraging by puku than shallow swamp. Grasslands were 12 times (Odds ratio = 12.19, *90% CI* = 1.66 to 89.37, *P* = 0.039) more likely to be fed within by puku than was shallow swamp. The chances of a site being used by puku during the LWS decreased by 2% (Odds ratio = 0.998, *90% CI* = 0.996 to 0.999, *P* = 0.009) with every 10 mm increase in grass height. A 10% increase in grass cover increased the odds of a foraging site being used by puku by 41% (Odds ratio = 1.041, *90% CI* = 1.03 to 1.06, $P < 0.001$). A 10% increase in grass greenness decreased the odds of puku utilizing a foraging site by 57% (Odds ratio = 0.943, *90% CI* = 0.92 to 0.97, *P* = 0.001).

Habitat type and grass cover were included in the model best suited to predicting habitat use by lechwe during the LWS (Model 2, Hosmer & Lemeshow $\chi^2 = 8.04$, D.F. = 8, *P* = 0.429: Pearson $\chi^2 = 39.66$, D.F. = 1, $P < 0.001$; **Table 3**). Specificity of was 94% and sensitivity was 55% giving an overall model correct classification of 82%. The interface zone was 8 (Odds ratio = 7.745, *90% CI* = 2.48 to 24.23, *P* = 0.003) times more likely to be used for foraging by lechwe, during the LWS, than shallow swamp. The odds of lechwe foraging within low lying floodplains was 67% (Odds ratio = 0.329, *90% CI* = 0.14 to 0.77, *P* = 0.030) lower than the odds of foraging within shallow swamp. The odds of lechwe foraging within high lying floodplains was 68% (Odd ratio = 0.316, *90% CI* = 0.13 to 0.79, *P* = 0.038) lower than the odds of foraging within shallow swamp. The odds of lechwe foraging within grasslands was 7 times (Odds ratio = 7.086, *90% CI* = 1.95 to 25.73, *P* = 0.012) the odds of lechwe foraging within shallow swamp. The odds of a foraging site being used by lechwe increased by 59% (Odds ratio = 1.059, *90% CI* = 1.04 to 1.08, $P <$ 0.001) for every 10% increase in grass cover.

High water season. The best fitting model (Model 3, Hosmer & Lemeshow $\chi^2 =$ 1.89, *D.F.* = 8, *P* = 0.984; Pearson $\chi^2 = 12.75$, *D.F.* = 1, $P < 0.001$; **Table 4**) predicting habitat use by puku during the HWS included grass height and grass cover. Specificity of the model was at 68% and sensitivity of the model was 89%, giving an

overall model correct prediction rate of 81%. The model showed that a 10 mm increase in grass height reduced the odds of that site being used by puku by 4% (Odds ratio = 0.996, *90% CI* = 0.994 to 0.998, *P* = 0.001). A 10% increase in grass cover at a foraging site increased the odds of use by puku by 51% (Odds ratio = 1.051, *90% CI* = 1.03 to 1.08, *P* <0.001).

Grass greenness was the only variable entered into the best fitting model (Model 1, Hosmer & Lemeshow χ^2 = 1.61, *D.F.* = 6, *P* = 0.952; Pearson χ^2 = 77.85, *D.F.* = 1, *P* <0.001; **Table 4**) for predicting habitat use by lechwe during the HWS. Model 1 therefore fit the data most adequately and had a model specificity of 100%, sensitivity 88%, and an overall correct model prediction rate of 95%. The model showed a foraging site was 37% (Odds ratio = 1.366, *90% CI* = 1.20 to 1.55, *P* <0.001) more likely to be used for foraging by lechwe for every 1% increase in grass greenness.

3.3.2 Comparative habitat use of puku and lechwe

The distance to water at puku and lechwe foraging sites differed significantly between species depending on the season (**Figure 26,** *F* = 4.313, *D.F.* = 2, *P* = 0.014). There was no significant difference between the distance to water of puku (*Mean* = 150 m, *95% CI* = 100.9 to 199.5, *SE* = 24.8) and lechwe (*Mean* = 85 m, *95% CI* = 56.2 to 113.4, *SE* = 14.36) foraging sites during the LWS. Lechwe foraging sites were 83 m closer to water than were available sites (*Mean* = 168 m, *95% CI* = 149.8 to 185.5, *SE* = 8.99) during the LWS. During the HWS, puku (*Mean* = 154 m, *95% CI* = 103.53 to 204.49, *SE* = 25.37) typically fed 138 m further from water than lechwe (*Mean* = 16 m, *95% CI* = 8.3 to 23.9, *SE* = 3.81) and 68 m further from water than sites that were available (*Mean* = 86 m, *95% CI* = 71.2 to 101.1, *SE* = 7.55). Lechwe foraged in sites that were on average 70 m closer to water than available sites during the HWS.

Depending on the season, grass height at puku and lechwe foraging sites was significantly different between these two herbivore species (**Figure 27**, F = 13.334, $D.F.$ = 2, P <0.001). Grass height at puku foraging sites (*Mean* = 198 mm, *95% CI* = 169.56 to 225.8, *SE* = 14.17) was 59 mm taller than lechwe foraging sites (*Mean* = 139 mm, *95% CI* = 117 to 160.10, *SE* = 10.83), but did not differ significantly from availability (*Mean* = 248 mm, *95% CI* = 223.63 to 272.64, *SE* = 12.35) during the LWS. Grass height at lechwe foraging sites was 108 mm lower than availability during the LWS. During the HWS grass height was not significantly different between puku (*Mean* = 237 mm, *95% CI* = 205.96 to 267.52, *SE* = 15.47) and lechwe foraging sites (*Mean* = 252 mm, *95% CI* = 208.01 to 295.93, *SE* = 21.53). Grass height at puku foraging sites was 251 mm shorter than availability (*Mean* = 488 mm, *95% CI* = 442.66 to 533.91, *SE* = 23) during the HWS. Grass height at lechwe foraging sites was 236 mm shorter than available sites during the HWS.

There was a significant interactive effect between season and species in the level of visual obstruction at foraging sites (**Figure 28**, F = 22.091, $D.F.$ = 2, P <0.001). During the LWS visual obstruction did not differ significantly between puku (*Mean* = 11%, *95% CI* = 8.26 to 13.5, *SE* = 1.32) and lechwe (*Mean* = 6%, *95% CI* = 3.29 to 8.69, *SE* = 1.36), or puku and available (*Mean* = 11%, *95% CI* = 9.26 to 12.82, *SE* = 0.9) foraging sites. Visual obstruction at lechwe foraging sites was 5% lower than availability during the LWS. Visual obstruction at puku foraging sites was 26% higher during the HWS (*Mean* = 37%, *95% CI* = 30.92 to 43.58, *SE* = 3.18) compared to the LWS, but was not significantly different from availability (*Mean* = 46%, *95% CI* = 42.46 to 50.13, *SE* = 1.93) during this season. During the HWS visual obstruction at lechwe foraging sites (*Mean* = 11%, *95% CI* = 6.84 to 14.37, *SE* = 1.84) was 26% lower than at puku foraging sites and 35% lower than at available foraging sites.

There was season dependent variation in grass greenness between puku, lechwe, and available foraging sites (**Figure 29**, F = 12.863, $D.F.$ = 2, P <0.001). Grass

greenness did not differ significantly between puku (*Mean* = 71%, *95% CI* = 68.78 to 73.38, *SE* = 1.16), lechwe (Mean = 75%, *95% CI* = 72.46 to 76.84, *SE* = 1.1), or available (*Mean* = 74%, *95% CI* = 72.77 to 75.77, *SE* = 0.76) foraging sites during the LWS. Grass greenness at puku foraging sites during the HWS (*Mean* = 62%, *95% CI* = 56.71 to 66.55, *SE* = 2.47) was 9% lower than the LWS, 19% lower than lechwe foraging sites (*Mean* = 81%, *95% CI* = 78.26 to 83.55, *SE* = 1.30), and 15% lower than at available foraging sites (*Mean* = 77%, *95% CI* = 74.86 to 79.51, *SE* = 1.17).

Depending on the season, there were significant differences in the level of grass cover at puku, lechwe, and available foraging sites (**Figure 30**, $F = 9.162$, *D.F.* = 2, $P < 0.001$). Grass cover at puku (*Mean* = 69%, *95% CI* = 64.55 to 72.57, *SE* = 2.02) foraging sites was 11% higher than availability (*Mean* = 58%, *95% CI* = 54.91 to 59.99, *SE* = 1.28) during the LWS. Grass cover at lechwe (*Mean* = 76%, *95% CI* = 71.80 to 80.64, *SE* = 2.22) foraging sites was 18% higher than availability, but did not differ significantly from puku foraging sites. Grass cover was 22% lower at puku foraging sites during the HWS (*Mean* = 47%, *95% CI* = 40.38 to 52.54, *SE* = 3.06) compared to the LWS, and 26% lower than at lechwe foraging sites (*Mean* = 73%, *95% CI* = 64.51 to 80.64, *SE* = 3.95). Grass cover at puku foraging sites did not differ significantly from availability during the HWS. Grass cover at lechwe foraging sites was 19% higher than availability (Mean = 54%, 95% CI = 49.66 to 58.04, SE = 2.11) during the HWS.

There was significant season dependent variation in the level of shrub cover at puku, lechwe and available foraging sites ($F = 23.086$, *D.F.* = 2, $P < 0.001$). Shrub cover did not vary significantly between puku (*Mean* = 0%, *95% CI* = -0.04 to 0.25, *SE* = 0.07), lechwe (*Mean* = 0%, *95% CI* = -0.23 to 0.70, *SE* = 0.23), or availability (*Mean* = 0.5%, 95% *CI* = 0.17 to 0.95, *SE* = 0.20) during the LWS. Seasonal shrub cover at puku foraging sites was 23% higher during the HWS (*Mean* = 23%, *95% CI* = 18.04 to 27.58, *SE* = 2.40) compared to the LWS. Shrub cover at puku foraging sites during

the HWS was 23% higher than at lechwe (*Mean* = 0%, *95% CI* -4.66 to 4.66, *SE* < 0.001), and 10% higher than available (Mean = 13%, 95% CI = 9.81 to 16.03, SE = 1.57) foraging sites.

The level of tree cover at puku, lechwe and available foraging sites differed significantly depending on the season ($F = 7.674$, $D.F. = 2$, $P < 0.001$). Neither puku nor lechwe fed in sites with tree cover during the LWS. Tree cover at puku foraging sites was 3% higher during the HWS (*Mean* = 3%, *95% CI* = 1.77 to 4.74, *SE* = 0.75) compared to the LWS, and matched availability (Mean = 2%, 95% CI = 1.12 to 2.49, SE = 0.34) during the HWS. Lechwe did not feed in areas with tree cover during the HWS.

3.3.3 Used population range estimation

Seasonal population range estimates may be underestimated during the HWS due to the limited accessibility of the Kabulabula, Puku Flats, and Lechwe Flats study sites. Seasonal used population range sizes differed widely between puku and lechwe **(Figures 31 & 32)**. The population range of puku during the LWS was estimated to be 9.3 km^2. The population range of lechwe during the LWS was estimated to be 6.2 km^2. The population range of puku increased in size from the LWS to the HWS, reaching 12.9 km^2. The population range of lechwe decreased from the LWS to the HWS, to a mean area of 4.1 km^2.

3.4 Discussion

Procurement of essential resources is a driving force in habitat selection by animals (Bowyer *et al*. 1998). Combined to the need to forage, animals may be faced with a risk of predation. Our understanding of the foraging ecology of species may therefore benefit through melding concepts of foraging efficiency to those of predator evasion (Ferguson *et al*. 1988; Bowyer *et al*. 1998). An optimal foraging strategy

would then be one which reduces the predation to forage ratio while enhancing reproductive fitness (Lacher *et al*. 1982; Mangel & Clark 1986; Brown *et al*. 1999). This may ideally be attained by selection of habitats presenting foods with high nutritive value and low predation risk. Conversely, such animal would seek to avoid habitats with low food value and high predation risk. In reality these features often conflict, and herbivores are faced by interplay between obtaining required foods while mitigating predation risk.

During the LWS, puku and lechwe were not recorded as foraging within shrubland, woodland, or termitaria. Puku and lechwe therefore showed strong avoidance of these habitats during the LWS. Grass greenness was lower in the upland habitats compared to the floodplain habitats, and the reduced visibility within the upland habitat types, due to the structural components of shrub and tree cover, would likely have inflated the risk of predation to puku and lechwe. A study conducted by Valeix *et al*. (2009) on African herbivores (including zebra, buffalo, warthog, wildebeest, kudu, giraffe, impala, and steenbok (*Raphicerus campestris*)) showed a strong preference for open habitat types with increased visibility when in the presence of lions. Avoiding foraging within habitats of low visibility would have reduced the risk of predation on puku and lechwe by ambush predators such as lion (*Panthera leo*) and leopard (*Panthera pardus*). Previous studies on puku (De Vos 1965; Goldspink *et al*. 1988; Dipotso & Skarpe 2006) and lechwe (Rees 1978; Williamson 1990) have also indicated towards a trend in avoidance of low visibility habitats.

Distance to water may have also played a role in avoidance of shrubland, woodland, and termitaria habitats, with these habitats generally being of greater distance from water compared to floodplain habitats. Valeix *et al*. (2007) and Valeix et al. (2009) reported distance to water as being the main influence in herbivore selection of habitats in the Hwange National Park, Zimbabwe. The motivation for avoiding upland habitats, due to their respective distances from water, may have been stronger

for lechwe than for puku. The reason being, lechwe have been previously documented as utilizing shallow water for escape terrain (Williamson 1990).

In northern Botswana, the LWS coincides with the late or hot dry season. Grass quality is generally of lower quality during dry periods with leaf material being brown and/or senescent. Crude protein concentrations often decline with increasing levels of fibre as grasses become senescent over the course of the dry season (Owen-Smith 1982; Macandza *et al*. 2004). Due to the higher ground water levels of floodplain environments (Hughes 1988) grasses growing within these habitats were able to retain greenness and nutritive value long into the dry season. *Cynodon dactylon,* the most commonly available grass species within the floodplains, remained green within the floodplains throughout the year (Dipotso & Skarpe 2004). Although not empirically tested in this study, the assumption was made that grasses within floodplain habitats were of higher quality than those growing in upland habitats. It is likely that puku and lechwe avoided shrubland, woodland, and termitaria habitats based on the quality of forage within these habitats. By feeding within habitats of higher food quality coupled to high levels of visibility, puku and lechwe conform to optimal foraging theory during the LWS.

Puku and lechwe were similar in their selection of the interface zone for foraging during the LWS. Habitats defined as the interface zone were more likely to be utilized by puku and lechwe than any other habitat type during the LWS. The interface zone was used for foraging with greater frequency, by both species, than was expected from availability. These findings match those of lechwe in the Linyanti Swamp, Botswana (Williamson 1990). The interface zone was defined as the area of wet land between dry ground and the waters edge. Due to the high soil moisture, grasses growing in this zone maintain greenness and nutrition for longer periods compared to other habitats (Williamson 1990). Due to grazing pressure by not only puku and lechwe but also other species (e.g. elephant, buffalo, zebra, wildebeest, impala, hippo, Pers. Obs.) maintained low levels of grass height within the interface

zone. Feeding within the interface zone would have allowed puku and lechwe to ingest high quantities of nutritious grass relative to bite size, while maintaining low predation risk.

A noticeable difference in the use of floodplain habitats between puku and lechwe, during the LWS, was the use or avoidance of shallow swamp. Puku avoided foraging within shallow swamp, utilizing the habitat less often than predicted from availability. Lechwe foraged within shallow swamp in accordance with availability, which was slightly higher than expected when compared to the findings of Williamson (1990). Puku have not previously been documented as foraging within shallow swamp (De Vos 1965; Von Richter & Osterberg 1977; Goldspink *et al.* 1998; Dipotso & Skarpe 2006) possibly due to the perceived threat by crocodiles. The avoidance of shallow swamp by puku may explain the curious finding of grass greenness decreasing the likelihood of a foraging site being used by puku during the LWS. Since the greenest grasses were found within shallow swamp habitats, avoidance of this habitat by puku may have directly influenced the odds ratio for grass greenness.

Puku were selective of grass height and grass cover at foraging sites, during the LWS. By being selective to grass height and grass cover, it appeared that puku were attempting to maximize their ingestion rate relative to the size of their mouths. Bite volume is dictated by mouth width and depth. Puku have relatively small mouths and by forging in sites dominated by dense grass cover in the height range of 170 - 226 mm may have allowed optimal feeding rates. Lechwe also based selection of foraging sites on grass cover, with increases in cover increasing the odds of utilization. Lechwe were however, less specific in regards to grass height at foraging sites during the LWS. This may have been due to the larger body size of lechwe (118 kg) compared to puku (77 kg). With a relatively larger mouth size, we may expect lechwe to be slightly less specific in the selection of grass height. Although the relationship between grass height and selection of feeding sites was not significant for

lechwe, the foraging sites of lechwe were typically composed of shorter grass than those of puku during the LWS.

Although slight, the differences in body size (Geist 1974) and the morphology and function of the digestive system (Gordon & Illius 1988) may have also contributed to the difference in precision in acceptance of foraging sites (Macandza 2009) by puku and lechwe. Smaller bodied animals have relatively higher metabolic requirements per unit body weight than larger animals (Gordon & Illius 1988). Smaller bodied animals should therefore occupy habitats providing higher quality diets (Bell 1969; Jarman 1974) or occupy habitats allowing maximal rates of ingestion of resources. Greater selectivity towards grass height and cover at foraging sites selected by puku was expected from niche breadth theory, which predicts that low density species use a narrower range of resources than high density species (based on the assumption that higher selectivity for grass height and cover reduces the quantity of suitable habitat and resources available to puku).

During the HWS, puku foraged within grasslands and shrublands more than what was expected from availability. Results from the logistic regression suggest that puku foraging within these habitats was more due to necessity, rather than preference. Foraging sites located within grasslands or shrublands did not increase or decrease the odds of utilization by puku during the HWS, indicating that puku were feeding within these sites because no other habitats were available. Neither puku (Goldspink *et al*. 1998; Dipotso & Skarpe 2006), lechwe (Rees 1978; Williamson 1980), nor kob (Modha & Eltringham 1976; Fischer & Linsenmair 2001) have been reported to seasonally use shrubland habitats. The puku population of northern Botswana thus appeared to utilize shrublands with greater frequency than should be expected – based on studies on *Kobus* species elsewhere. Puku remained consistent in selection of foraging sites based upon grass height and grass cover during the HWS. Foraging sites with shorter denser grass were more likely to be selected for foraging by puku. Average grass height at puku foraging sites during the HWS was far greater than that encountered during the LWS. The uniform increase in grass height was most likely a

result of increased grass growth due to the start of the rainy season. This increase in the height of the grass could explain the increased specificity of puku for grass height during the HWS. As the height of the grass in the surrounding environment increased, puku would have had to intensify their search for grasses in the height range necessary for maintenance of optimal intake rates.

During the HWS puku were recorded as feeding in areas with higher levels of shrub cover than what was available to them. An increase in shrub cover at puku foraging sites from the LWS to the HWS was expected as the availability of floodplain habitats diminished and puku moved into upland habitats. Foraging in areas of reduced visibility during the HWS is likely to have increased the risk to predation. Puku mortality due to lion and leopard, appeared to increase dramatically during the HWS. Although the effects of predation were not evaluated during this study, the number of predator related deaths of puku, that reported by safari guides working in the area, increased substantially during the HWS. I also personally found a greater proportion of puku carcasses during the HWS compared to the LWS. Since puku do not seem to be limited nutritionally (see Chapter 2), the effects of increased predation risk during the HWS appeared to be the factor limiting the population of puku within the Chobe National Park.

Lechwe did not move from the floodplains to the upland areas during the HWS. Lechwe preferred to concentrate foraging within the few available areas of dry land within the inundated floodplains. Due to the reduction in available floodplain habitat, most inter-specific competitors (such as puku) moved into the upland habitats during the HWS. This reduction in the level of inter-specific competition may have then allowed lechwe to select for green nutritious grass without risk of being out-competed. As mentioned previously, the HWS coincided with the wet season. The green-flush of growing grass may have added to the increase in the specificity of lechwe to grass greenness during the HWS.

Puku maintained the distance to water of foraging sites from the LWS to the HWS by feeding within shrublands adjoining the waters edge. Conversely, the mean distance to water of lechwe foraging sites deceased from the LWS to the HWS. Although it has been reported that lechwe utilize shallow water as escape terrain (Rees 1978; Williamson 1990), it was not observed during this study. The decrease in the mean distance to water of lechwe foraging sites was most likely due to the increase in the level of the water and the decrease in available floodplain habitat.

Animals roam over areas that are large enough to satisfy needs for food, cover, and mating opportunities (Fischer & Linsenmair 2001). McNab (1963) suggested because energetic requirements rise with body size, that body weight and home range size are correlated. McNab (1963) further suggested that home range size could be estimated using the following formula: $A_{ha} = 2.7(M)^{0.63}$, where A_{ha} is home range size in hectares, and M is the mass of the animal. This formula however, took no account of the differences between herbivores and carnivores, leading Harestad & Bunnel (1979) to propose a modified equation for predicting the home range size of herbivores: $A_{ha} = 2.71(M)^{1.02}$. Using this formula, the estimated home range for puku should have been in the region of 228 ha (2.3 km^2), and that of lechwe in the region of 352 ha (3.5 km^2).

Since this study did not focus home range estimation from individuals but rather on the populations of puku and lechwe, we may assume that the range size of populations would be larger than those suggested above for individual animals. This assumption is based on the fact that the home range of individuals from a gregarious population share high levels of overlap with one another, and therefore the range of the population becomes increasingly large as the home ranges of individuals are added. The size of the population range established in this study did surpass those determined as being sufficient for individual home ranges that were estimated by the formula of Harestad & Bunnel (1979).

The ‘sub-population’ ranges of puku and lechwe within the Chobe National Park should in no way be viewed as distinct and independent from one another. An important limitation in population range estimation in this study was that I did not know if individual animals moved between sub-populations occupying the different study sites. If there was movement between sub-populations the size of the population ranges can be expected to be larger than those reported, because the MCPs would have incorporated those areas used for travel between study sites.

The estimated population ranges of puku and lechwe were more than double the estimated home ranges of kob in the Camoé National Park, Ivory Coast (Fischer & Linsenmair 2001), but roughly half the range reported for the puku population in the Kasanka National Park, Zambia (Goldspink *et al*. 1998). Goldspink *et al.* (1998) estimated the range of puku in Kasanka National Park from the area of occupied floodplains and dambos and not from individual animals.

Although population range size may be expected to be positively correlated to population size for some species, this did not appear to be the case for the *Kobus* genus, with individual species differing extensively in population density. The population size of puku in the Chobe National Park was estimated to be around 130 individuals (Dipotso & Skarpe 2006; Personal observations) giving a density of 10.08 km^{-2}, with the lechwe population at around 550 individuals (Personal observations) giving a density of 88.71 km^{-2}. Estimates place the population of kob in the Camoé National Park at 305 individuals with an estimated density of 1.1 km^{-2} (Fischer & Linsenmair 2001), and the population of puku in the Kasanka National Park at 613 individuals with a density of 35.93 km^{-2} (Goldspink *et al*. 1998).

The seasonal population ranges of puku where higher than those of lechwe and the influence of the flood waters appeared to have contrasting effects on the size of puku and lechwe ranges. Puku increased the size of the population range from the LWS to the HWS. The reaction of puku to the inundation of the floodplains was to spread out within the shrublands along the margins of the floodwaters. Spreading out in such a

manner, as opposed to concentrating within feeding areas when on the floodplains, probably served two purposes. Firstly, spreading out in such a manner reduces the level of intra-specific competition allowing individuals access to a greater quantity of the resources available, while still allowing individuals to maintain a close proximity to water. Secondly, while concentrating in groups is good in areas with high visibility (Hamilton 1971; Bertram 1978; Fischer & Linsenmair 2001), dispersion may enhance survival when visibility is low and groups are more conspicuous and easily detected by predators (Treisman 1975; Fischer & Linsenmair 2001).

Similar to lechwe in the Linyanti Swamp (Williamson 1990), the population range size of lechwe along the Chobe River contracted from the LWS to the HWS. As the floodwaters rose, and the availability of the floodplains decreased, lechwe moved with the rising waters and concentrated into exposed grassland areas within the floodplains for the duration of the high water period. This strategy, like puku, appeared to have two main advantages to lechwe. Firstly, during the HWS, the concentration of other animal species within the floodplains was greatly reduced – by remaining on the floodplains lechwe would have experienced reduced levels of inter-specific competition for resources. Although susceptible to intra-specific competition, the remaining exposed grassland habitats provided ample resources to maintain the lechwe population throughout the HWS. Secondly, concentrating into available grassland habitats within inundated floodplains allowed lechwe to maintain high levels of visibility, and utilize flooded areas as escape terrain from predators (Williamson 1990).

The LWS and HWS habitat use and population density of lechwe appeared to be consistent with the findings of Rees (1978) and Williamson (1990). While LWS habitat use by puku was consistent with the observations of Goldspink *et al*. (1998) and Dipotso & Skarpe (2006), HWS habitat use appeared to deviate from trends reported for puku (Goldspink *et al*. 1998; Dipotso & Skarpe 2006), lechwe (Rees 1978; Williamson 1990) and kob (Fischer & Linsenmair 2001). The prolonged

seasonal use of upland habitats by puku has not previously been reported, and seems to distinguish the Chobe population from those reported elsewhere. The estimated population density of puku with Chobe was low compared to that reported for puku in Kasanka National Park, Zambia (Goldspink *et al*. 1998), but was higher than that reported for kob in the Camoé National Park, Ivory Coast (Fischer & Linsenmair 2001).

In light of the findings reported above, increased predation risk to the puku population during the HWS would seem the most likely factor limiting the expansion of the population. Further research focusing specifically on the influence of predators on the Chobe puku population would be of great benefit to future management planning. Also, further comparative research specifically comparing habitat use of the Chobe puku population to populations within Zambia and Tanzania is recommended.

3.5 Key results

- Puku preferred to forage within the interface zone and grasslands during the LWS. Within these habitat types, puku preferred to forage in areas with short, green grass and high levels of grass cover. Lechwe preferred to forage within shallow swamp, the interface zone, and grasslands during the LWS. Areas with high levels of grass cover were selected by lechwe for foraging during the LWS.
- During the HWS when there was reduced availability of floodplain habitats, puku selected foraging locations based on grass height and grass cover while lechwe selected foraging sites based on grass greenness.
- The used population range of puku was larger across all seasons

CHAPTER 4

CONCLUSIONS AND MANAGEMENT IMPLICATIONS FROM THE STUDY ON THE COMPARATIVE DIET AND HABITAT SELECTION OF PUKU AND LECHWE ON THE CHOBE RIVER FLOODPLAIN, BOTSWANA.

4.1 Conclusion

The context of this study was the identification of possible factors contributing to the perceived low population density and distribution of puku (*Kobus vardonii*) within the Chobe National Park, Botswana. The aim of the study was to compare the resident population of puku to the closely related congeneric, lechwe (*Kobus leche*). The study broadly evaluated resource partitioning between puku and lechwe at differing hierarchical scales of resource selection.

The first level of resource selection to be evaluated was diet selection by puku and lechwe. Specific objectives relating to this portion of the study were: 1) to determine seasonal diet selection of puku and lechwe; 2) evaluate the level of dietary overlap between puku and lechwe across seasons; 3) determine a value of preference/acceptance for grass species in the diet of puku and lechwe; 4) identify relationships between the structure and phenological condition of plant species in the diet and the animal preferences for these plants; and 5) using faecal nutrient analyses, identify nutritionally critical and nutritionally stable periods for puku and lechwe.

The second level of resource selection evaluated in this study was habitat selection by puku and lechwe. Specific objectives assessed in regards to habitat selection were: 1) establish resource selection functions (RSF) for puku and lechwe; 2) investigate how the RSF changes in relation to the seasons; 3) analyze any differences between the RSF of puku and lechwe in each of the seasons; 4) determining the effects of

vegetative physical characteristics and topographical features on the RSF; 5) estimating and compare the home range size of puku and lechwe in each season.

The key questions pertaining to this study were: 1) are puku and lechwe mutually distinct in the selection of dietary components? and 2) how does differential diet selection impact each species nutritionally? and lastly, 3) do puku and lechwe utilize different habitat types within the broader landscape available to them?

Competition for food resources is likely to occur between sympatric grazers if there is no separation between animals at the grass species or grass features level (Macandza *et al.,* 2004). Grazing herbivores have been shown to differ in preference of grass height for grazing while showing distinct overlap in the grass species consumed (Bell 1970; Jarman & Sinclair 1979). Overlap between grazers has also been found in the height of grasses eaten by short grass grazers (Arsenault & Owen-Smith 2008), suggesting differential preference for grass height alone may not adequately separate grazers with similar preferences for grass height.

Nutritional requirements needed for growth and maintenance are the overriding factors determining the diet of any animal species. In accordance with optimal foraging theory, food items are accepted if the benefit derived from obtaining them outweigh the cost of search for and ingesting a more profitable food item (Stephens & Krebs 1986, in Owen-Smith 2005).

Resource availability theory (Gaston & Kunin 1997; Gregory & Gaston 2000) and niche breadth theory (Brown 1984) led me to investigate, in Chapter 2, the dietary composition of puku and lechwe. I also measured the faecal concentrations of nitrogen and phosphorus to gain an indication of the nutritional fitness of each species.

Key findings of chapter 2 were:

1. The diets of puku and lechwe along the Chobe River were composed entirely of grass species. Puku had a slightly wider dietary breadth than that of lechwe (although sample size was not controlled for), but despite this, both species shared high levels of dietary overlap, from 84% during the LWS to 90% during the HWS, as assessed using Pianka's Niche Overlap Index (Pianka 1973).
2. Despite the high levels of overlap, the diets of puku and lechwe differed somewhat in important features. Puku consumed greater quantities of *V. nigritana* and *Brachiaria* species, with lechwe consuming greater quantities of *P. mauritianus*. This suggests that puku and lechwe are at least partially ecologically separated by diet composition and with respect to the microhabitat conditions where these particular grass species were most prevalent.
3. Puku were more selective towards height and greenness of grass species than were lechwe. During the LWS, the odds of acceptance of a grass species by puku increased as grass height decreased. LWS acceptance of grass species by lechwe was not influenced by any of the phenological characteristics measured by this study. During the HWS acceptance of grass species by puku became dependent on grass greenness and height, while acceptance by lechwe became dependent on grass height. Grass was typically greener at lechwe foraging sites, and this may account for the lack of influence of grass greenness on acceptance.
4. Puku and lechwe were indistinguishable in faecal N and P throughout the year. The concentration of faecal P in puku did however vary significantly between seasons. Puku faecal P levels appeared to increase during the HWS as a result of the onset of the rainy season and the corresponding 'green flush'. Neither species appeared to be deficient in N or P at any stage through the year. Since puku did not appear to be limited nutritionally, the indication is that predation may be the factor limiting the distribution of puku in the Chobe National Park.

It has been suggested that high density species utilize a wider range of habitat types compared to low density species which use a narrow range of habitats (Brown 1984; Rosenzweig & Lomolino 1997). Some authors (see for example Seagle & McCraken 1986; Gaston & Kunin 1997) have also suggested a preference for habitats of low availability by low density animals. Body size theory further suggests that smaller bodied herbivores require higher quality food resources compared to larger herbivores (Bell 1970; Jarman 1974). Based on these observations, in Chapter 3 I investigated how puku and lechwe were able to coexist through differential habitat type use resulting in ecological resource partitioning.

Key findings from Chapter 3 were:

1. Both puku and lechwe showed preference for feeding within the interface zone and grasslands during the LWS. While puku showed strong avoidance of shallow swamp, lechwe were reported as utilizing shallow swamp in accordance with availability during the LWS. Differentiation in habitat use between puku and lechwe was most apparent during the HWS. Puku moved off the inundated floodplains into shrubland areas adjacent to the floodwaters while lechwe remained within the floodplains in areas that were isolated and remained exposed from the floodwaters.
2. In both seasons, puku were more selective towards the physical attributes of foraging sites than were lechwe. Grass greenness, height, and cover, all influenced the selection of foraging sites by puku during the LWS. Lechwe were only selective towards grass cover at foraging sites during the LWS. During the HWS, puku remained selective towards grass height and grass cover but were no longer selective to grass greenness. This may have been a result of the general increase in grass greenness throughout the region brought about by the rainy season. Conversely, lechwe showed preference towards grass greenness during the HWS only selecting grass species with comparatively elevated levels of greenness.

3. Despite lower population densities than lechwe, puku retained larger population ranges throughout the year. In reaction to the inundation of the floodplains, puku increased the size of their used range from the LWS to the HWS. By remaining in areas of exposed ground within the inundated floodplains, the population range of lechwe contracted from the LWS to the HWS. This suggests that puku and lechwe employ different strategies of habitat use during the HWS.

Overall, the results from this study showed significant overlap in the use of food and habitat types between puku and lechwe. Distinct resource partitioning was however apparent between species. Puku were more selective of grass greenness, cover, and height than were lechwe. Due to the greater selectivity in grass features, puku may have had to feed from a wider array of grass species compared to lechwe. The disparity in dietary breadth could also have resulted from puku moving into shrubland areas during the HWS where upland grass species were available. Puku however, appeared to be less constrained spatially and temporally than did lechwe. Clear partitioning of habitat use was evident during the HWS. Puku were able to transition from floodplain to shrubland habitat with no negative impact on nutrition. Lechwe, although not impacted nutritionally, were constrained spatially during the HWS as is evident from the contraction of the population range size. Puku and lechwe are able to coexist as congeneric species within the Chobe National Park through subtle partitioning of food and habitat resource use.

Since neither puku nor lechwe appeared to be deficient nutritionally, and since both species shared high levels of overlap of food and habitat resources, the indication is that predation may be the factor limiting the puku population. Puku and lechwe deviate in terms of their habitat use during the HWS. Lechwe remain on the floodplains in areas of high visibility and close proximity to escape terrain (water), while puku move into shrubland areas with low levels of visibility and elevated risk to predation. Reduced visibility in shrubland areas would allow greater concealment

of predators such as lion, leopard, hyena (*Crocuta crocuta*), and wild dog (*Lycaon pictus*), thereby increasing the risk of capture of puku.

4.2 Management implications

The motivation behind this study was the assertions made by Dipotso & Skarpe (2006) that the population of puku along the Chobe Riverfront should be considered vulnerable to local extinction. Because it appears that puku are not nutritionally limited, and since they share high levels of overlap in diet and habitat use with the more widespread lechwe, it is my recommendation that future management and research be directed at; 1) determining the impacts of predation, 2) expanding food resource and habitat comparisons to other areas within Botswana, and 3) compare the diet and habitat use of Chobe puku to the burgeoning puku populations of Kasanka National Park, Zambia. Specific management objectives should include:

- ✓ A direct comparative study on population density between Chobe and Kasanka puku populations. This study should also include the collection of data on calf survival.
- ✓ The implementation of an annual census of the puku population in order to obtain accurate, informative information on long-term population estimates. The annual census should include the collection of demographic data to indicate whether recruitment or survival is limiting the expansion of the puku population.
- ✓ Vegetative and habitat comparisons between the areas occupied by puku in Chobe and floodplain areas that i) occur further west along the Chobe River, ii) floodplains within the Okavango Delta, iii) floodplains on the Namibian side of the river. By examining this data we will be able to tell if puku are confined to their current distribution due to food and/or habitat limitations.
- ✓ Examine the direct and indirect effects of predation on the puku population during low water and high water periods.

- ✓ Determine the impact of increased tourism on the puku population and establish thresholds of concern pertaining to poaching. This data will reveal the influence of human pressure on the puku population along the Chobe River.

TABLES AND FIGURES

Figure 1: The distribution of puku, *Kobus vardonii* (map adapted from Kingdon, 1997, source www.ultimateungulate.com).

Figure 2: The distribution of lechwe, *Kobus leche* (map adapted from Kingdon, 1997, source www.ultimateungulate.com).

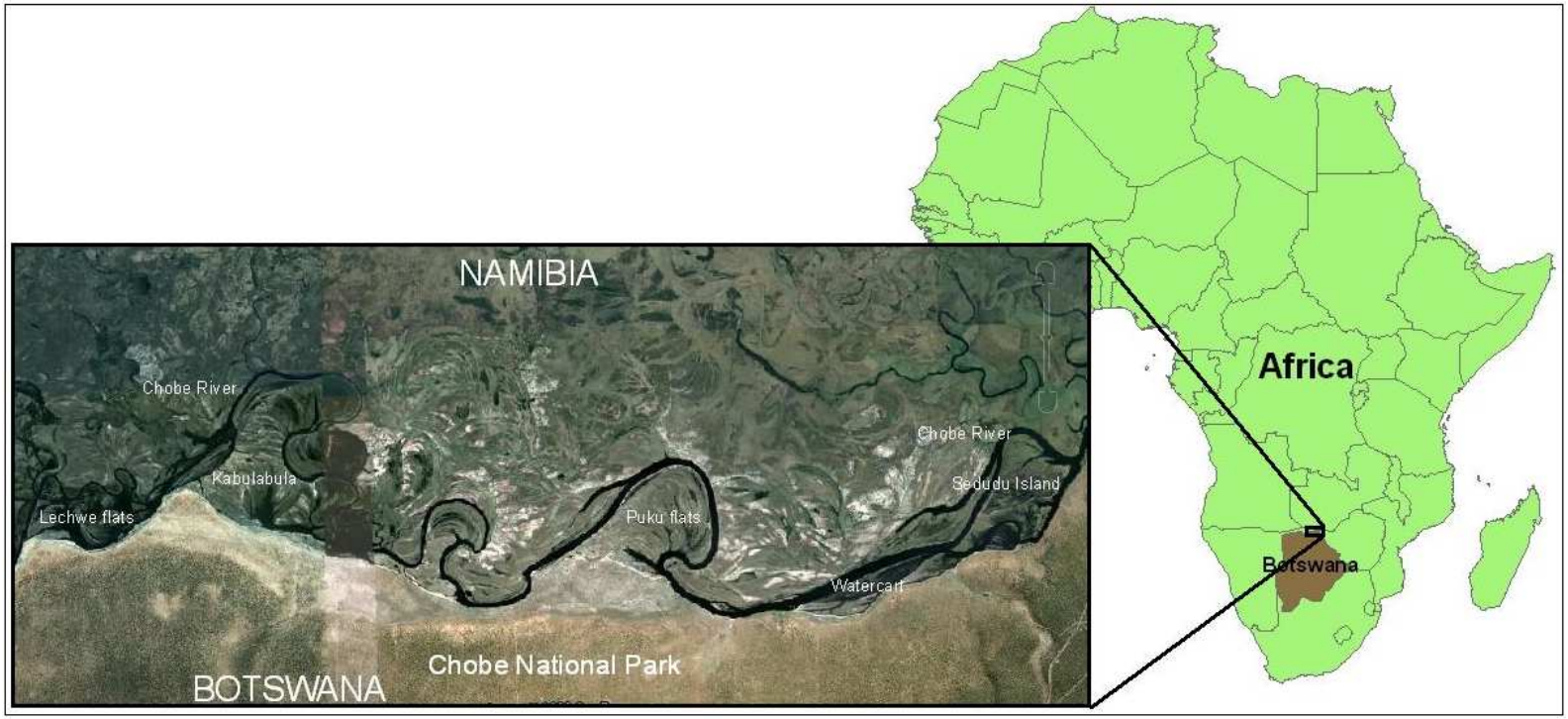

Figure 3: Location of the general study area along the Chobe River, Chobe National Park, Botswana.

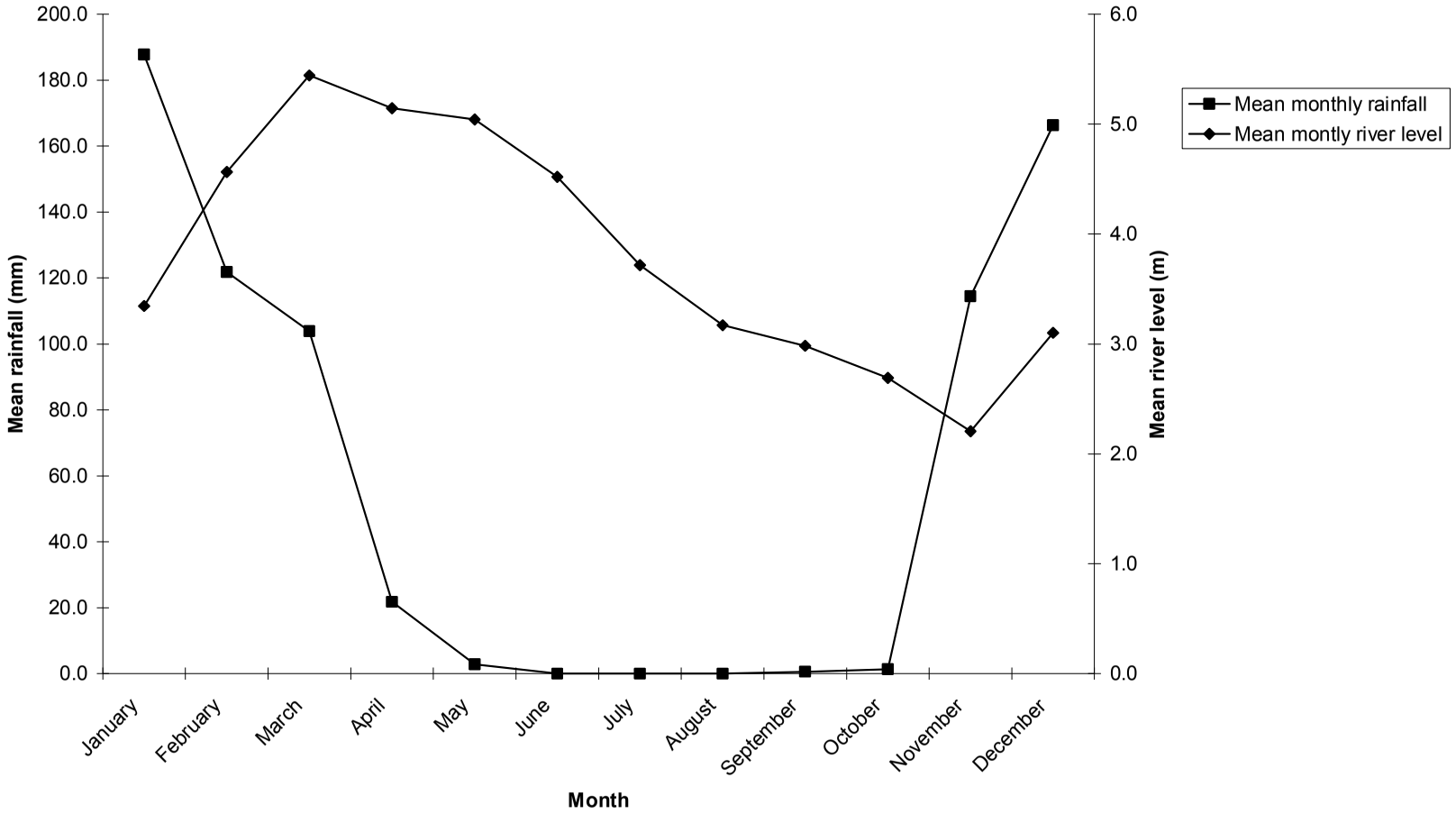

Figure 4: Mean monthly rainfall (period 2004 – 2009) and river levels (period 2005 – 2009) for Kasane, Botswana.

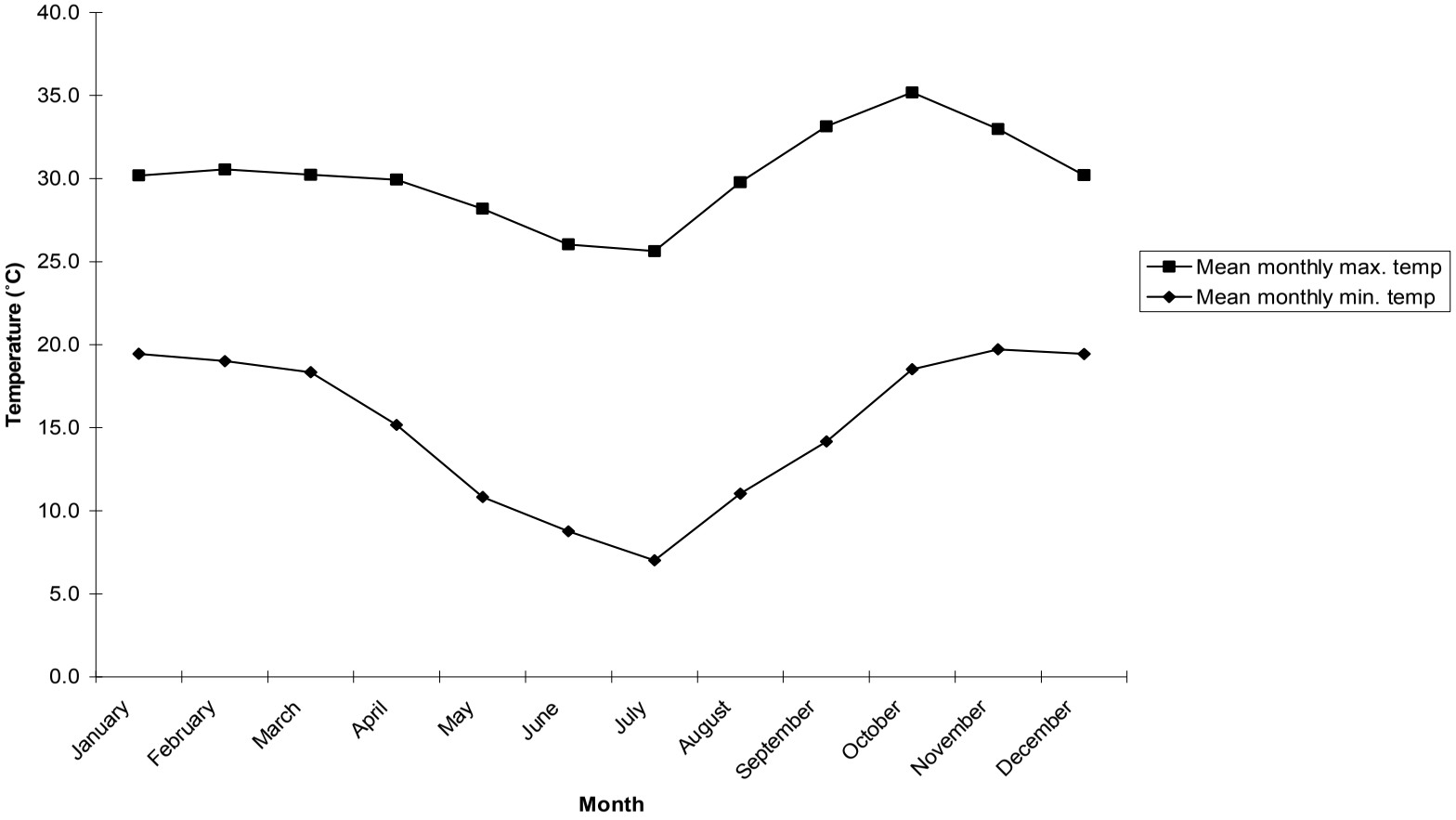

Figure 5: Mean maximum and minimum temperatures for Kasane (period 2003-2008).

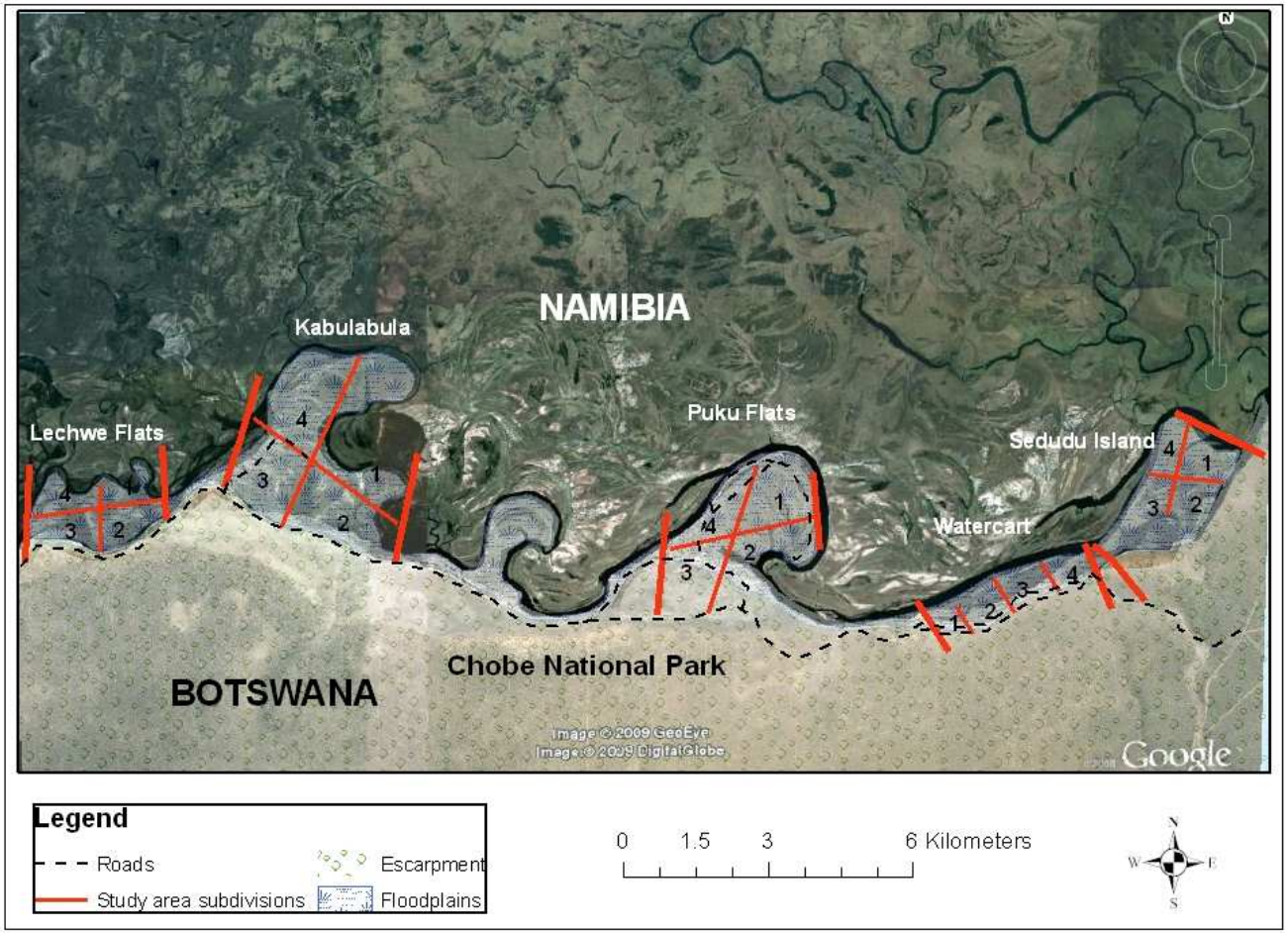

Figure 6: Location of the floodplains and Kalahari sand ridge (escarpment), with the subdivisions of the intensive study areas, along the Chobe River, Botswana.

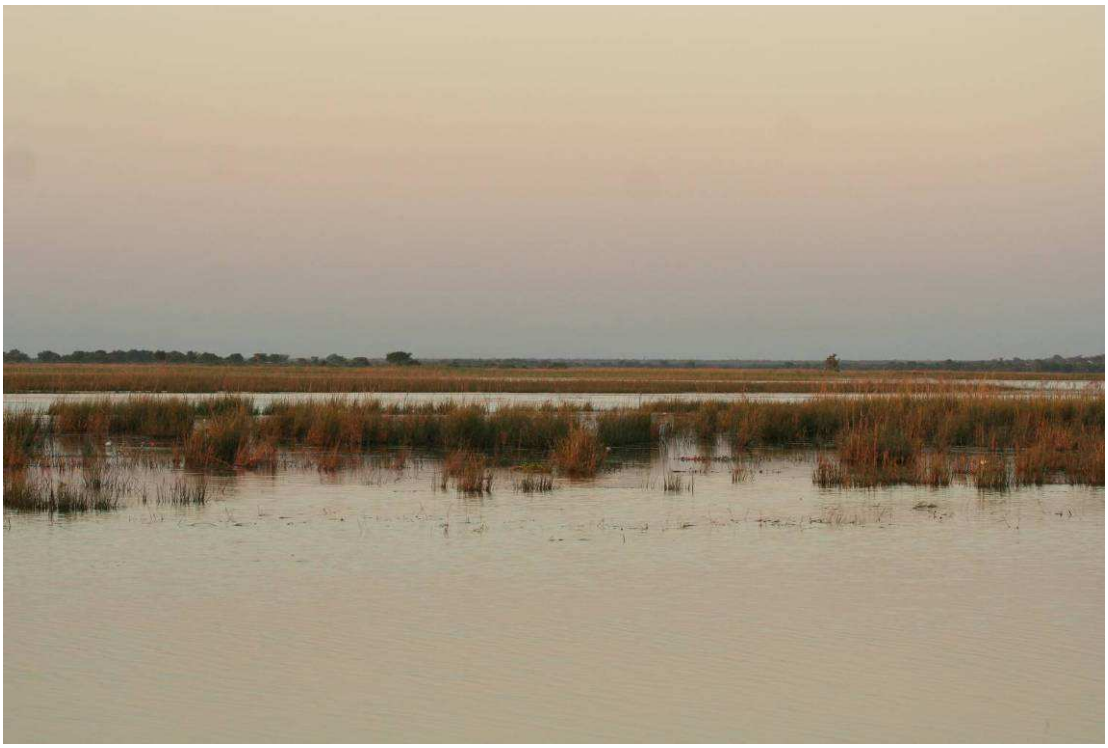

Figure 7: Typical flood plain environment along the Chobe River, Chobe National Park, Botswana. This photo was taken during the high water season.

Figure 8: A young male puku standing in typical *Combretum* shrubland, Chobe National Park, Botswana. This photo was taken during the dry season.

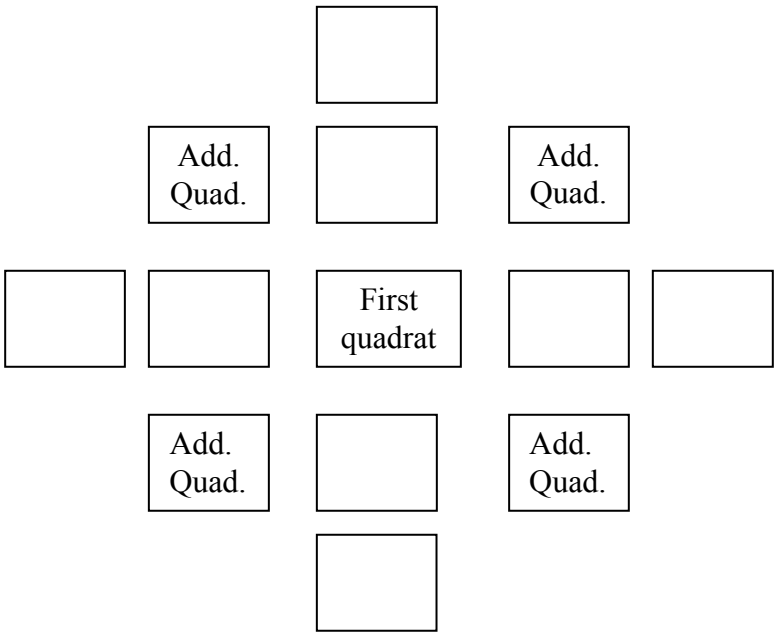

Figure 9: Distribution of quadrats within puku and lechwe foraging areas. The 'Add. Quad.' in the diagram represents additional quadrats.

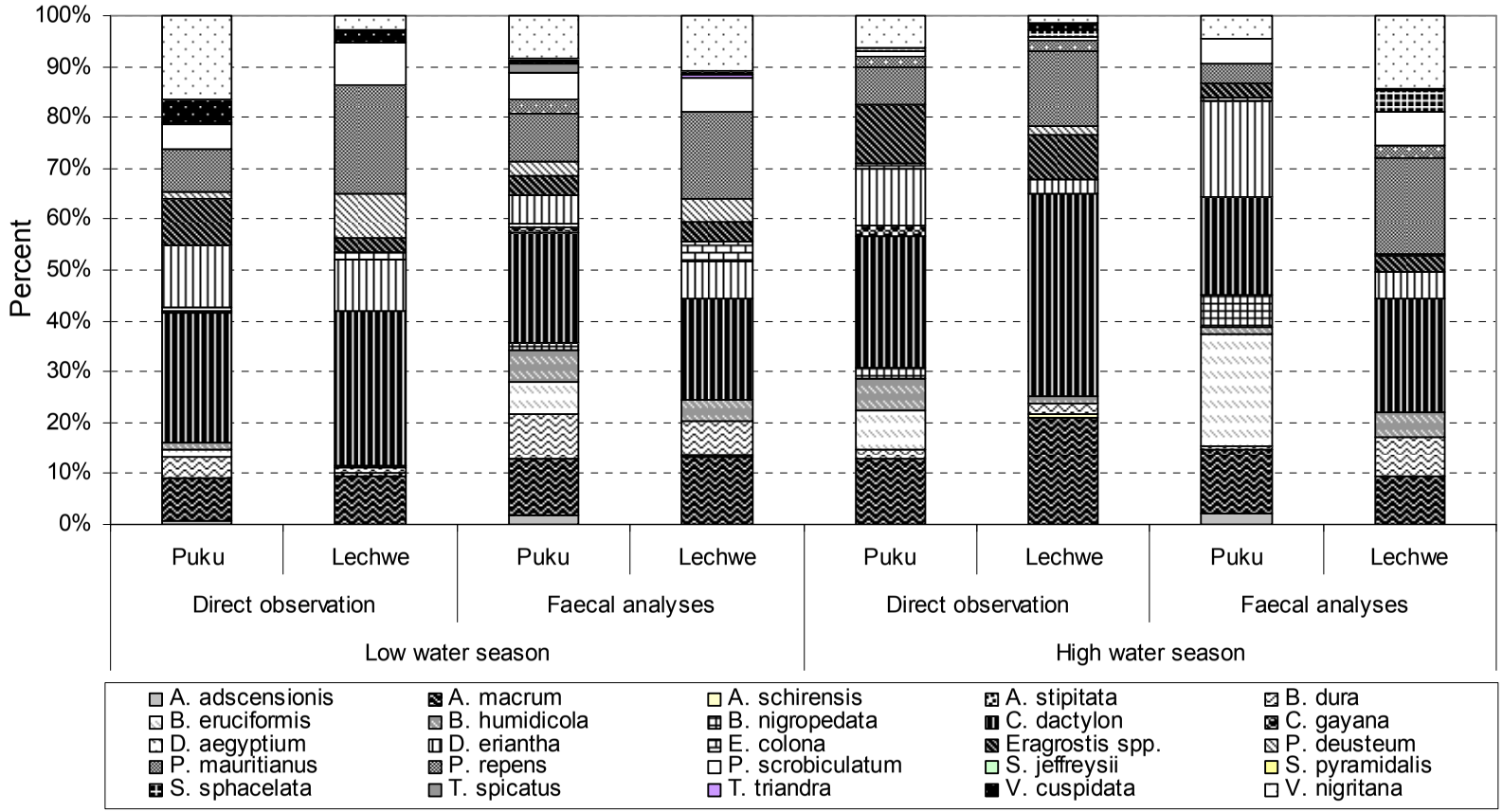

Figure 10: Seasonal proportions of grass species in the diets of puku and lechwe.

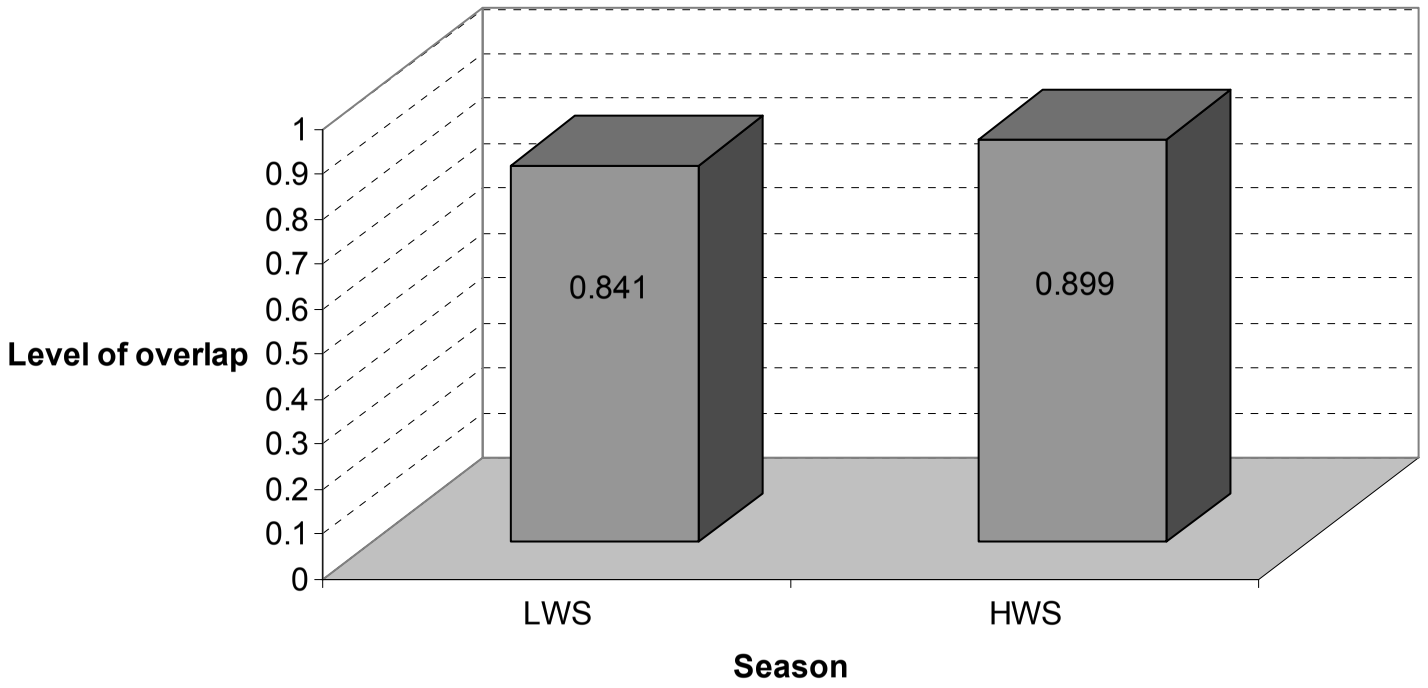

Figure 11: Seasonal level of dietary overlap between puku and lechwe.

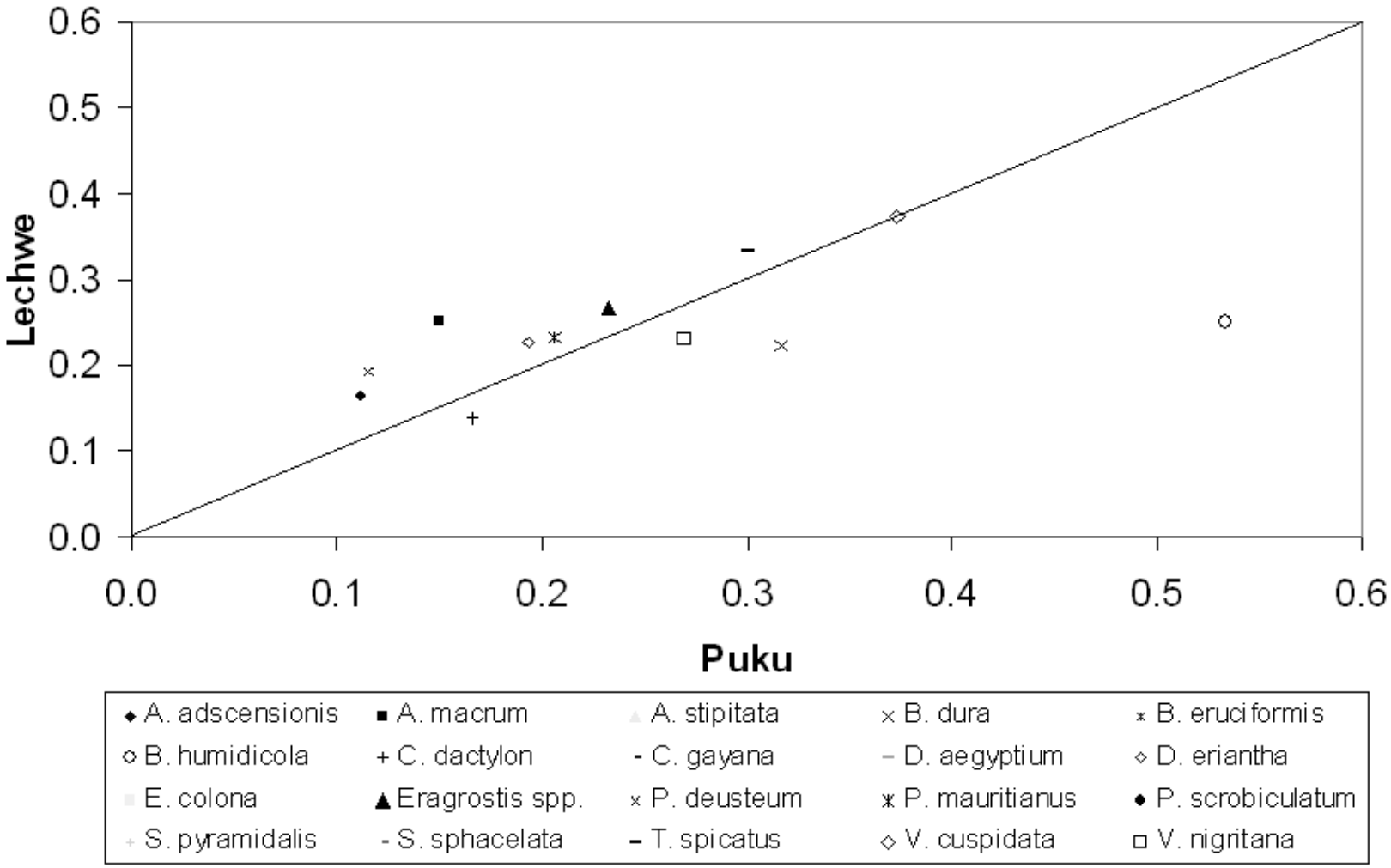

Figure 12: Plant-based acceptance values of grasses in the diets of puku and lechwe during the low water season.

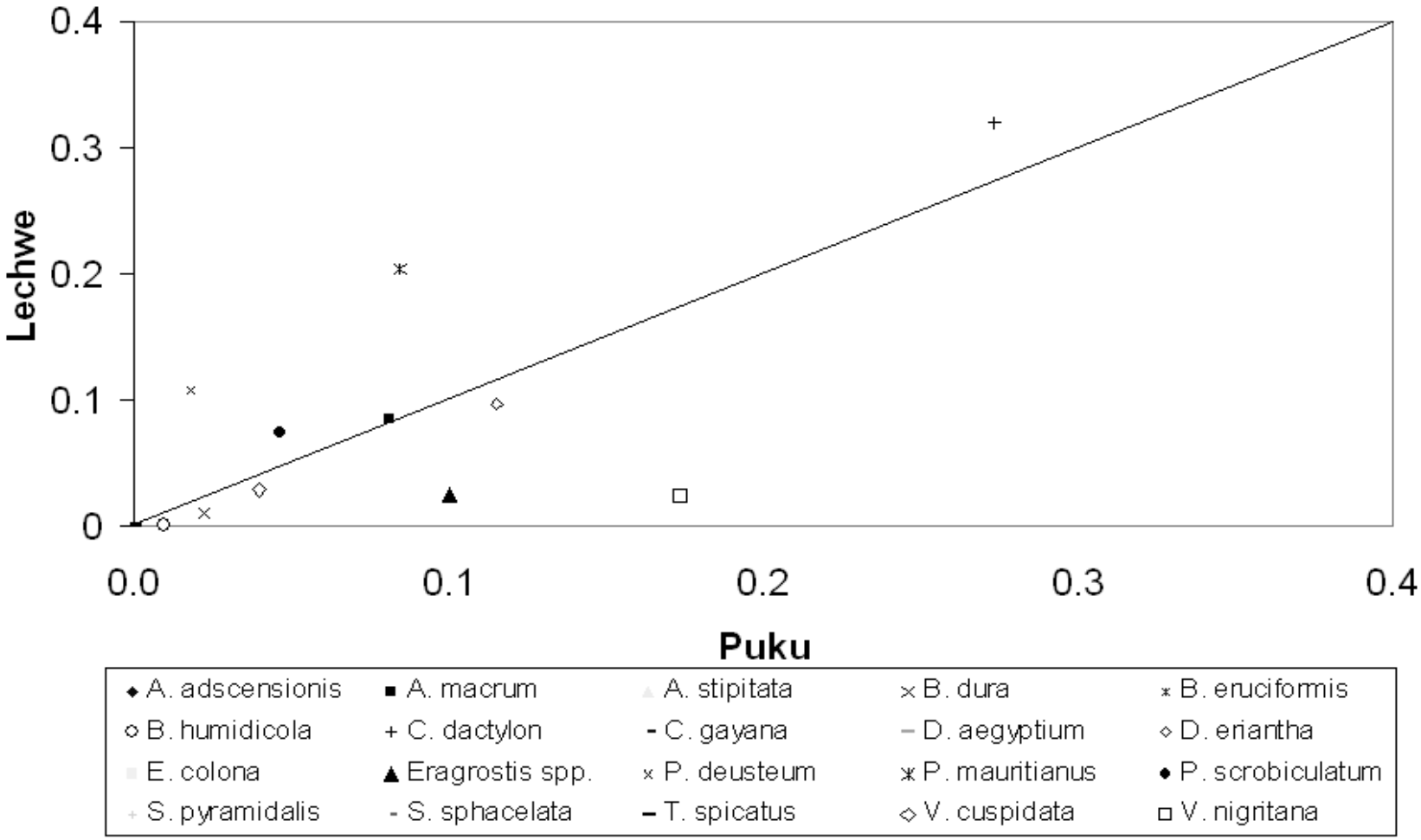

Figure 13: Plant-based availabilities of grasses in the diets of puku and lechwe during the low water season.

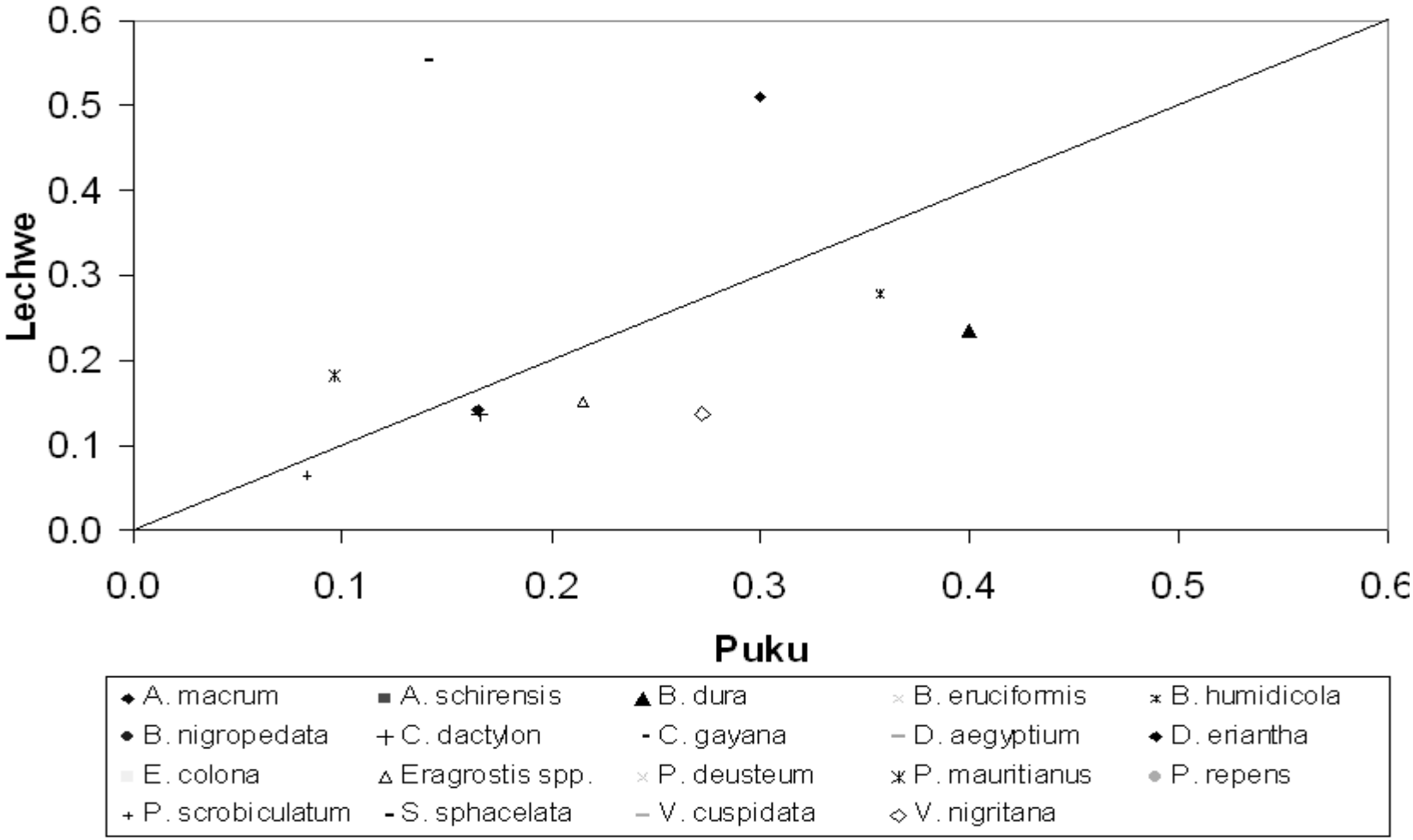

Figure 14: Plant-based acceptance values of grasses in the diets of puku and lechwe during the high water season.

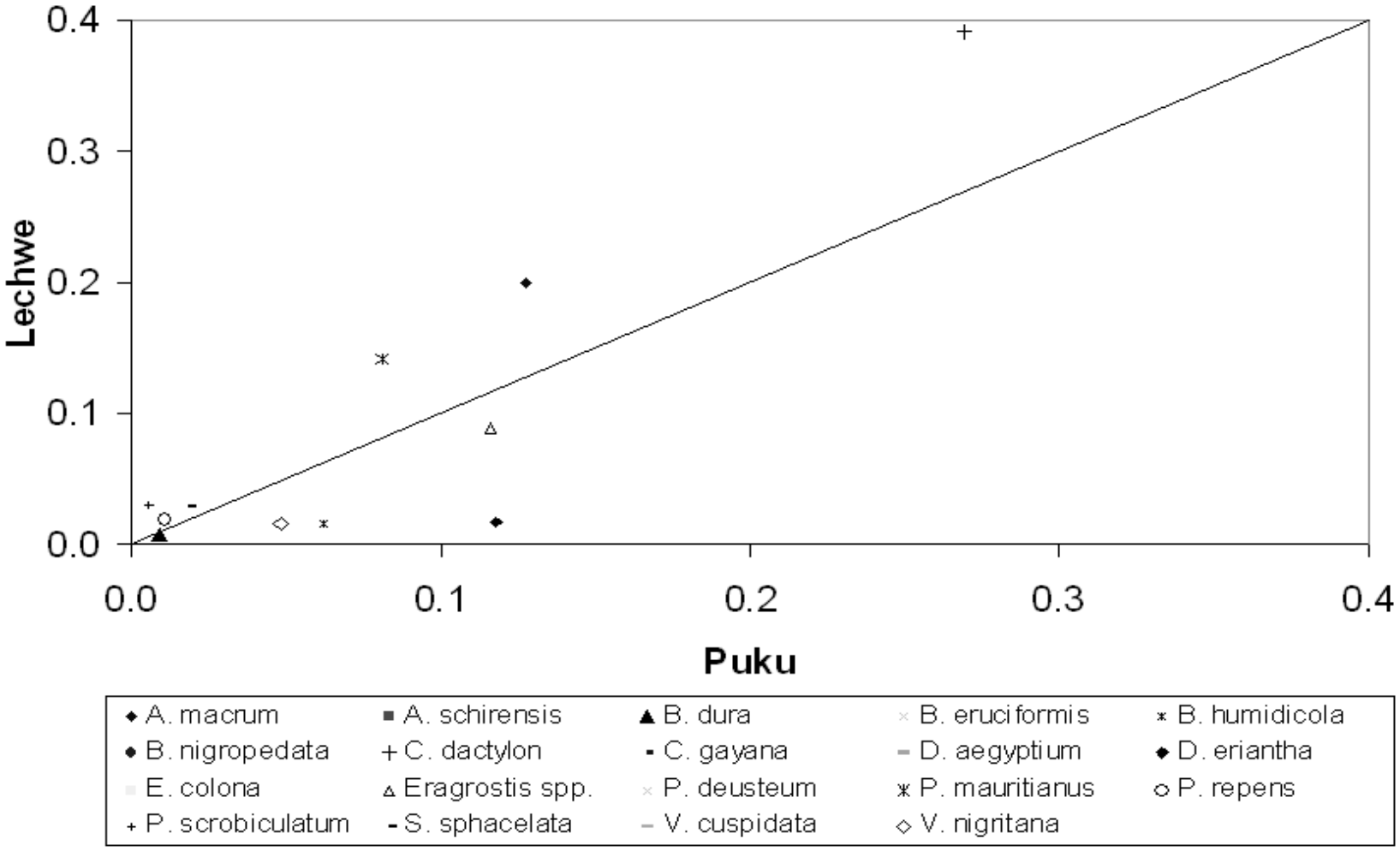

Figure 15: Plant-based availabilities of grasses in the diets of puku and lechwe during the high water season.

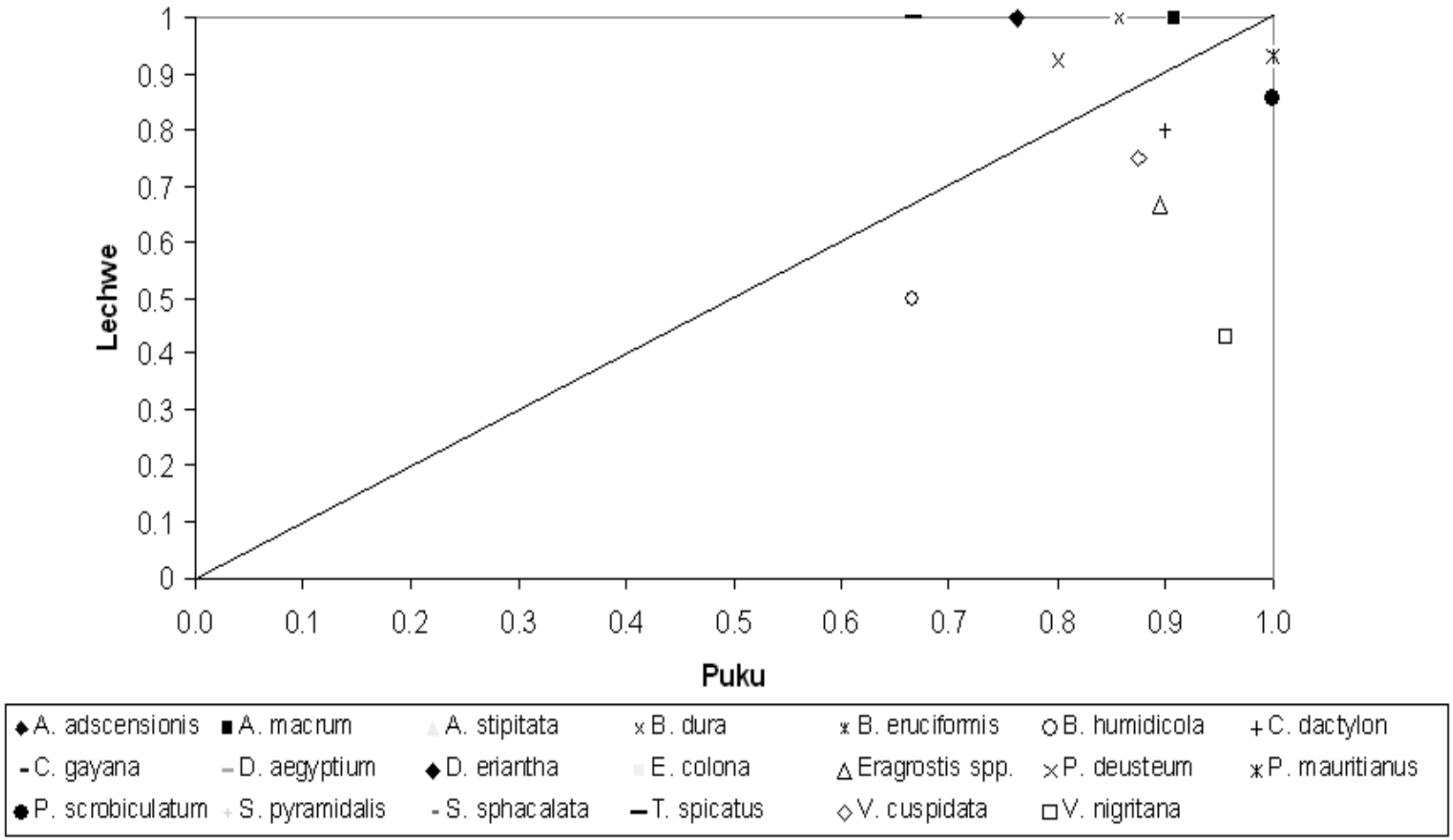

Figure 16: Site-based acceptance values of grasses in the diets of puku and lechwe during the low water season.

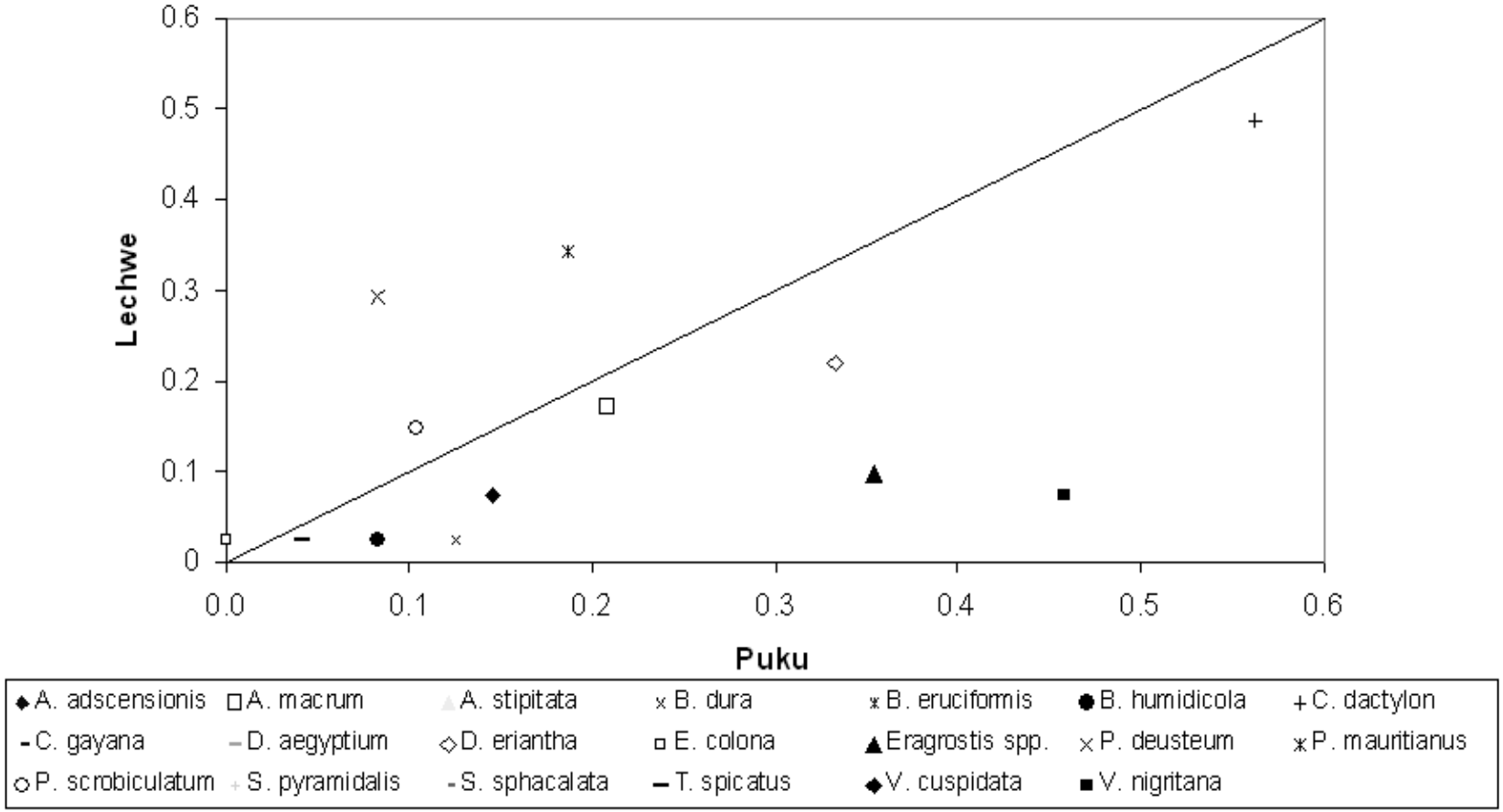

Figure 17: Site-based availabilities of grasses in the diets of puku and lechwe during the low water season.

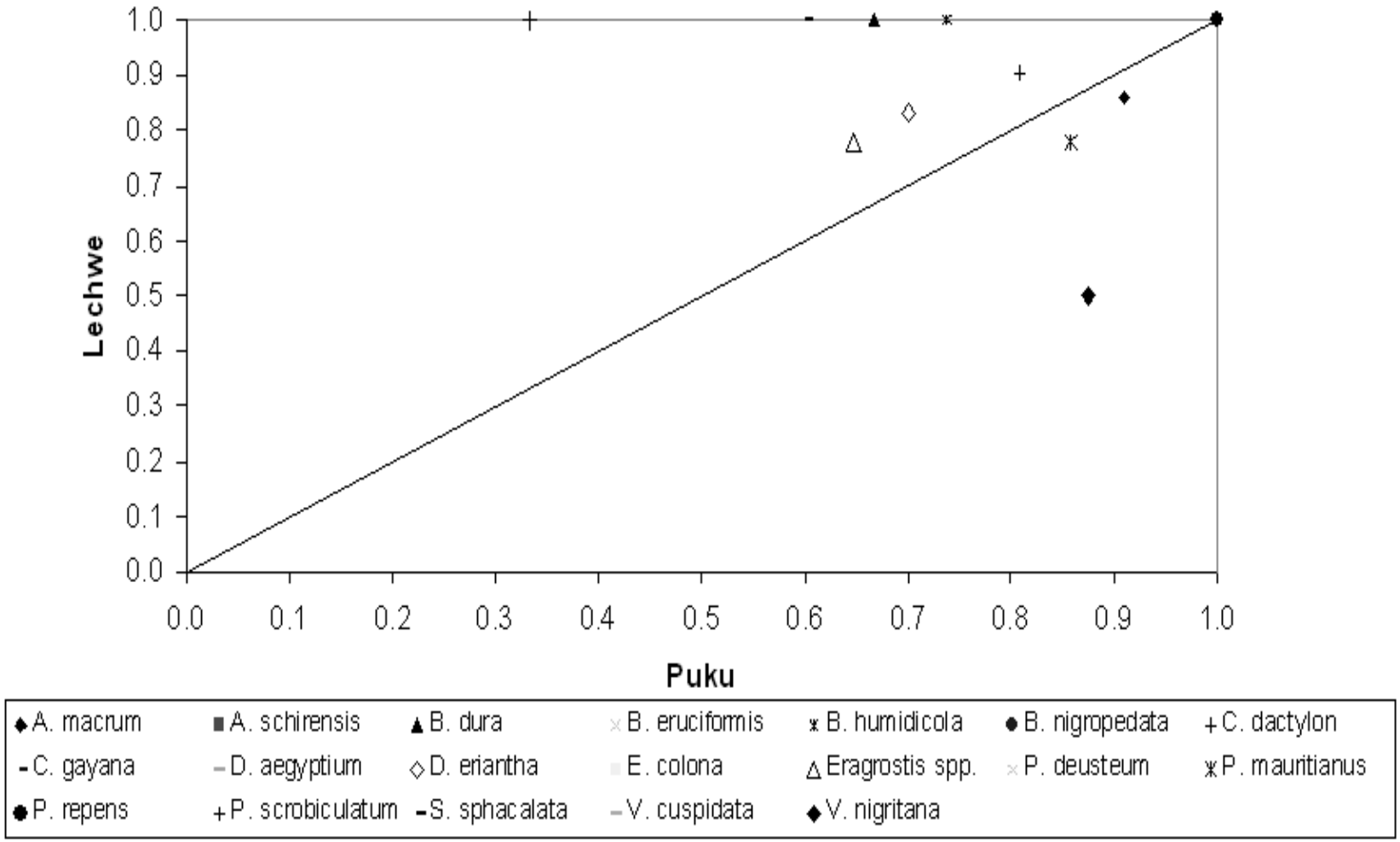

Figure 18: Site-based acceptance values of grasses in the diets of puku and lechwe during the high water season.

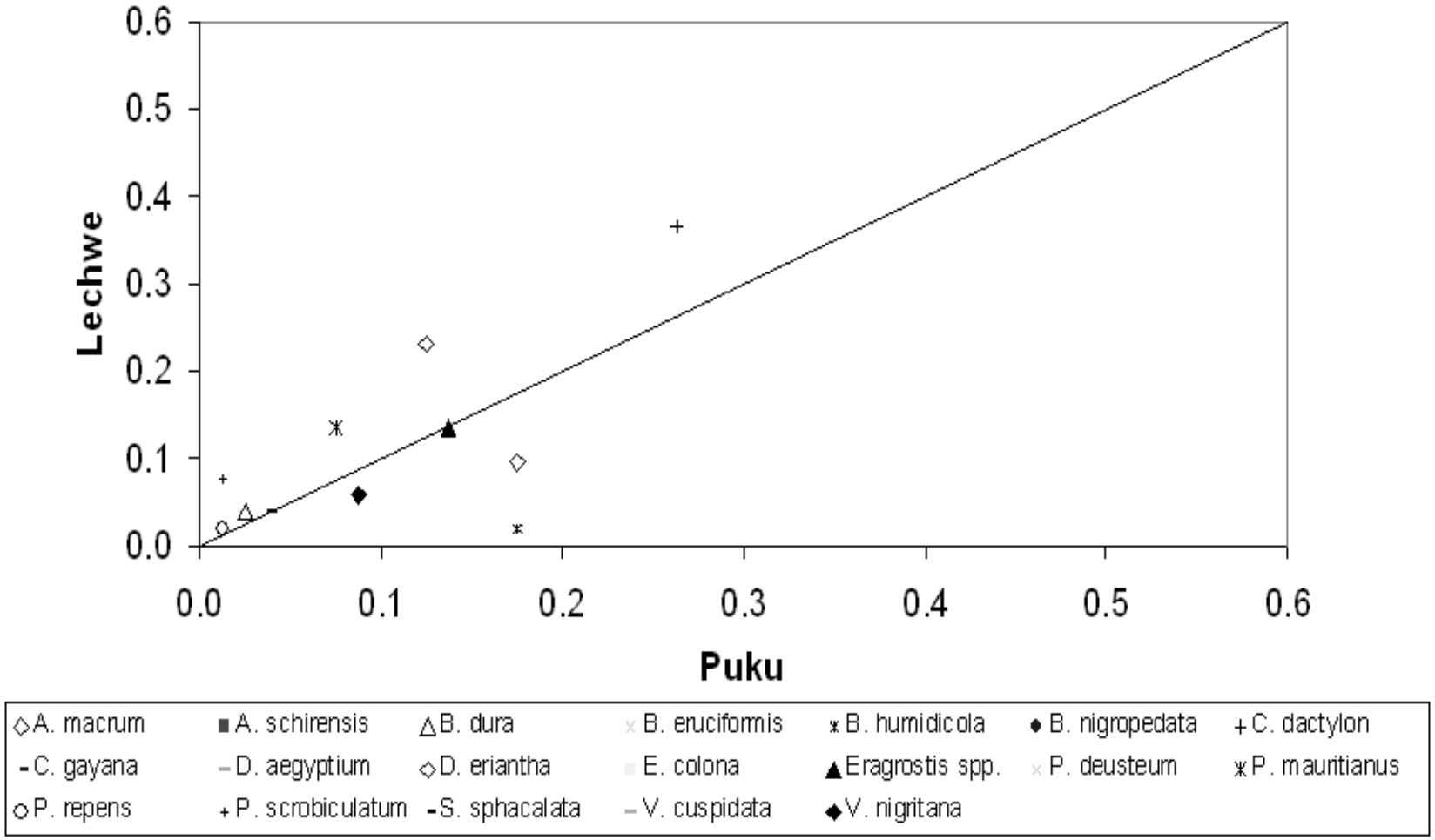

Figure 19: Site-based availabilities of grasses in the diets of puku and lechwe during the high water season.

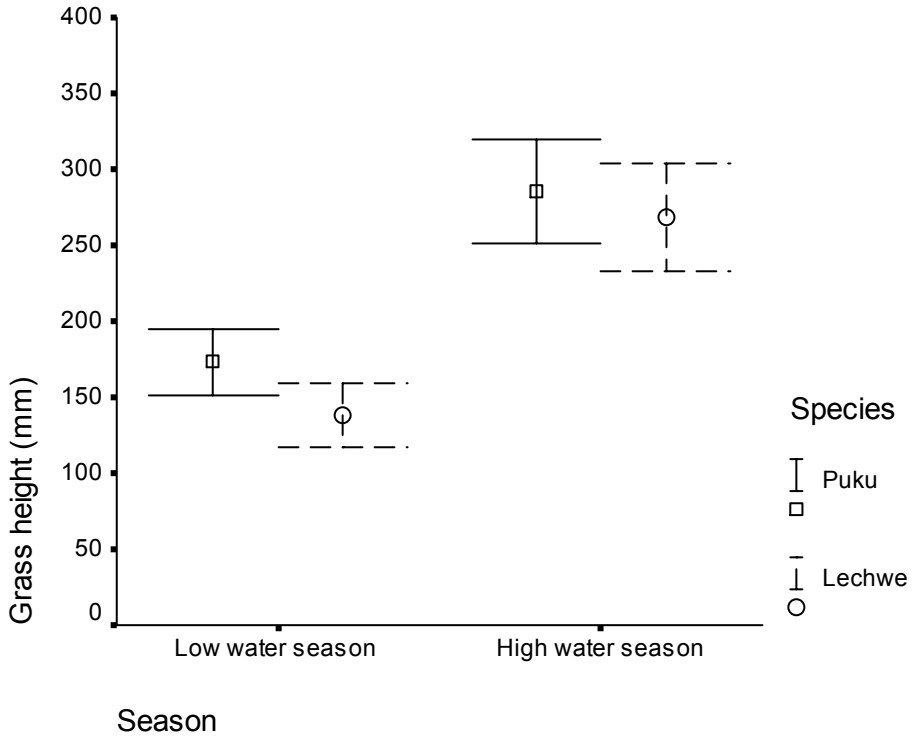

Figure 20: Average grass height at puku and lechwe foraging sites. Bars represent 95% confidence intervals.

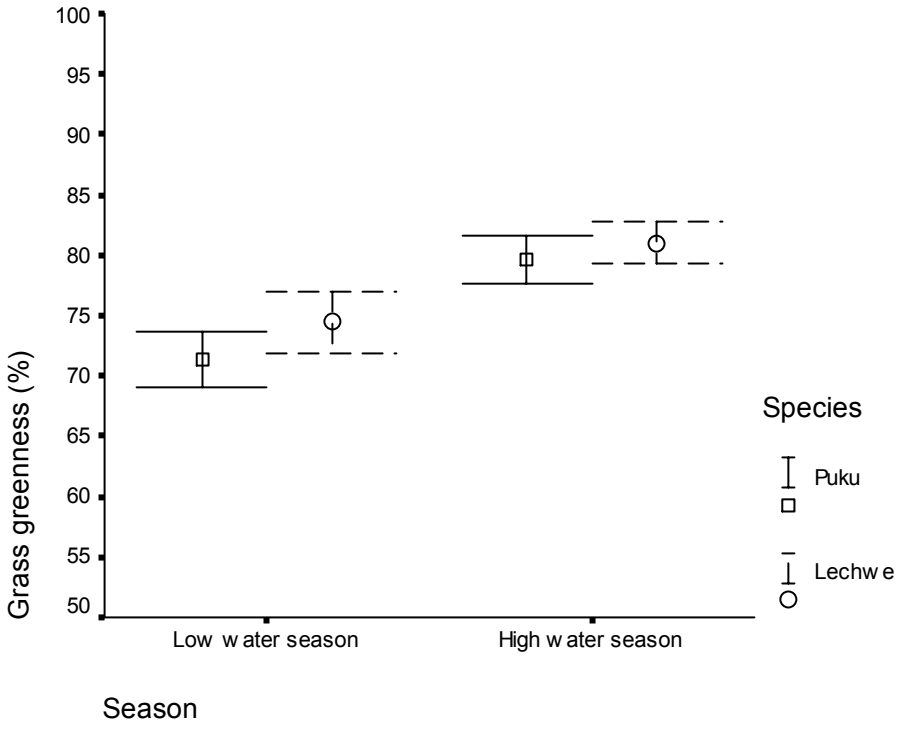

Figure 21: Average grass greenness at puku and lechwe foraging sites. Bars represent 95% confidence intervals.

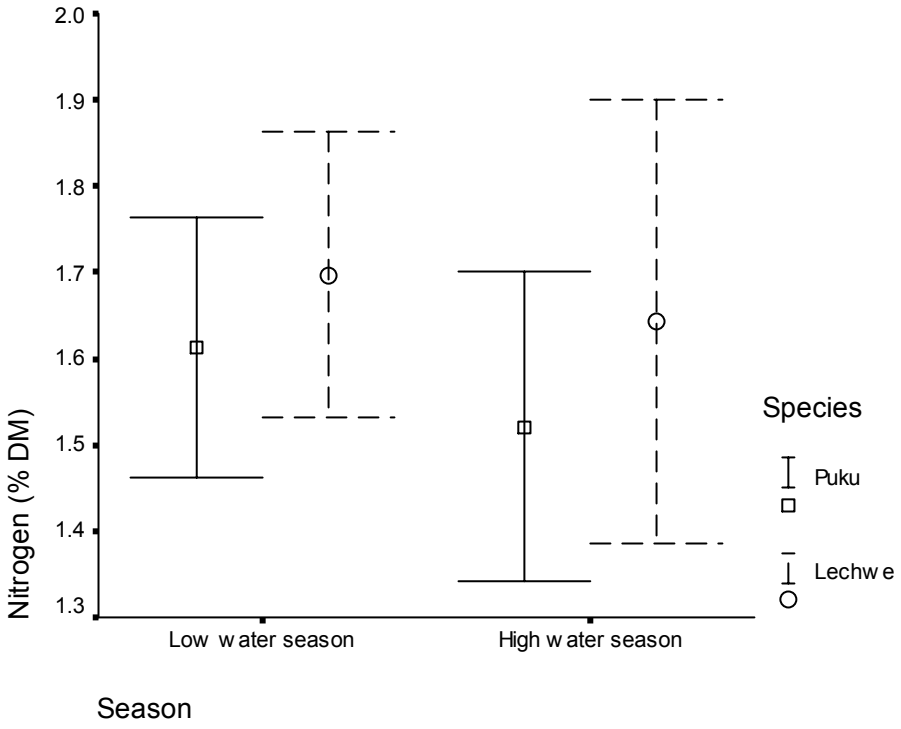

Figure 22: Seasonal faecal nitrogen levels for puku and lechwe. Bars represent 95% confidence intervals.

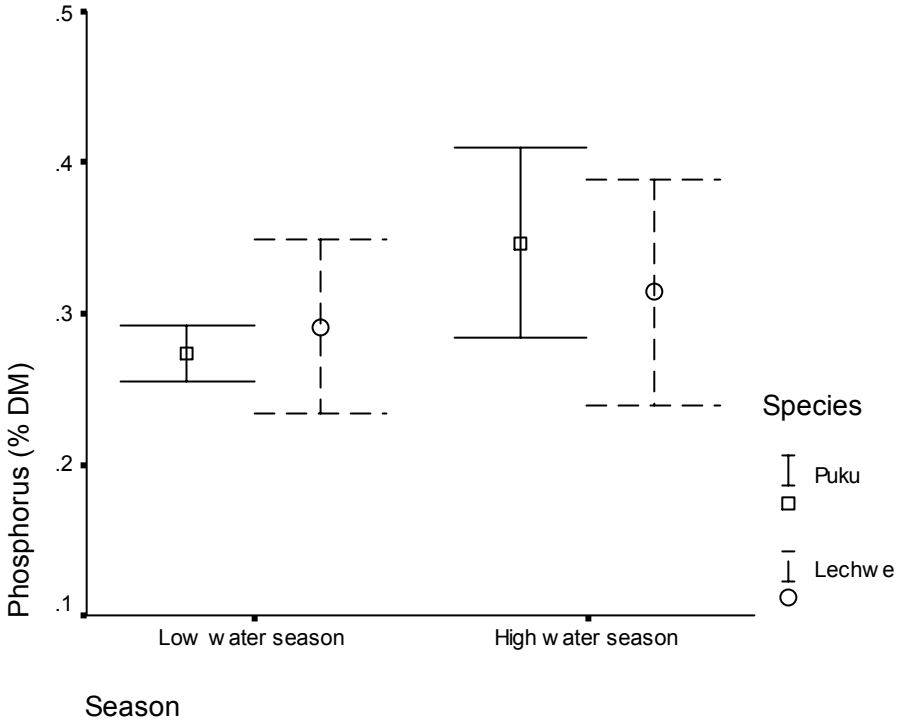

Figure 23: Seasonal faecal phosphorus levels for puku and lechwe. Bars represent 95% confidence intervals.

Table 1: List of variables used in the study of puku and lechwe habitat use within the Chobe National Park, Botswana.

Number	Variable	Abbreviation	Type	Value
1	Habitat type	habitat	Categorical	0 = Shallow swamp, 1 = Interface zone, 2 = Low lying floodplain, 3 = High lying floodplain, 4 = Grasslands, 5 = Shrublands, 6 = Woodlands, 7 = Termitaria
2	Distance to water	dist.wat	Continuous	Meters (m)
3	Grass height	grass.he	Continuous	Millimeters (mm)
4	Visual obstruction	vis.obs	Continuous	Percent (%)
5	Grass cover	grass.co	Continuous	Percent (%)
6	Shrub cover	shrub.co	Continuous	Percent (%)
7	Tree cover	tree.co	Continuous	Percent (%)
8	Grass greenness	grass.gr	Continuous	Percent (%)
9	Annual Hydrophytic	ann.hydr	Dichotomous	0 = Absent, 1 = Present
10	Annual Helophytic	ann.helo	Dichotomous	0 = Absent, 1 = Present
11	Annual Xerophytic	ann.xero	Dichotomous	0 = Absent, 1 = Present
12	Perennial Xerophytic	per.xero	Dichotomous	0 = Absent, 1 = Present
13	Perennial Helophytic	per.helo	Dichotomous	0 = Absent, 1 = Present
14	*Combretum spp.*	combretu	Dichotomous	0 = Absent, 1 = Present
15	Perennial Hydrophytic	per.hydr	Dichotomous	0 = Absent, 1 = Present
16	Annual or Perennial	ann.per	Dichotomous	0 = Absent, 1 = Present
17	*Croton megalaboris*	croton	Dichotomous	0 = Absent, 1 = Present
18	*Capparis tomentosa*	capparis	Dichotomous	0 = Absent, 1 = Present
19	*Erythroxylum zambesiacum*	erythrox	Dichotomous	0 = Absent, 1 = Present
20	*Baikea plurijuga*	baikea	Dichotomous	0 = Absent, 1 = Present

Table 2: List of the variables entered into each logistic model during each season, for puku and lechwe. The number of models produced in each logistic procedure are also listed.

	LWS	**HWS**
Variables entered into models	Habitat type Distance to water Grass height Visual obstruction Grass cover Grass greenness Annual-Helophytic Perennial-Xerophytic Perennial-Helophytic Perennial-Hydrophytic	Habitat type Distance to water Grass height Visual obstruction Grass cover Grass greenness Perennial-Hydrophytic
No. of models for puku	8	5
No. of models for lechwe	6	3

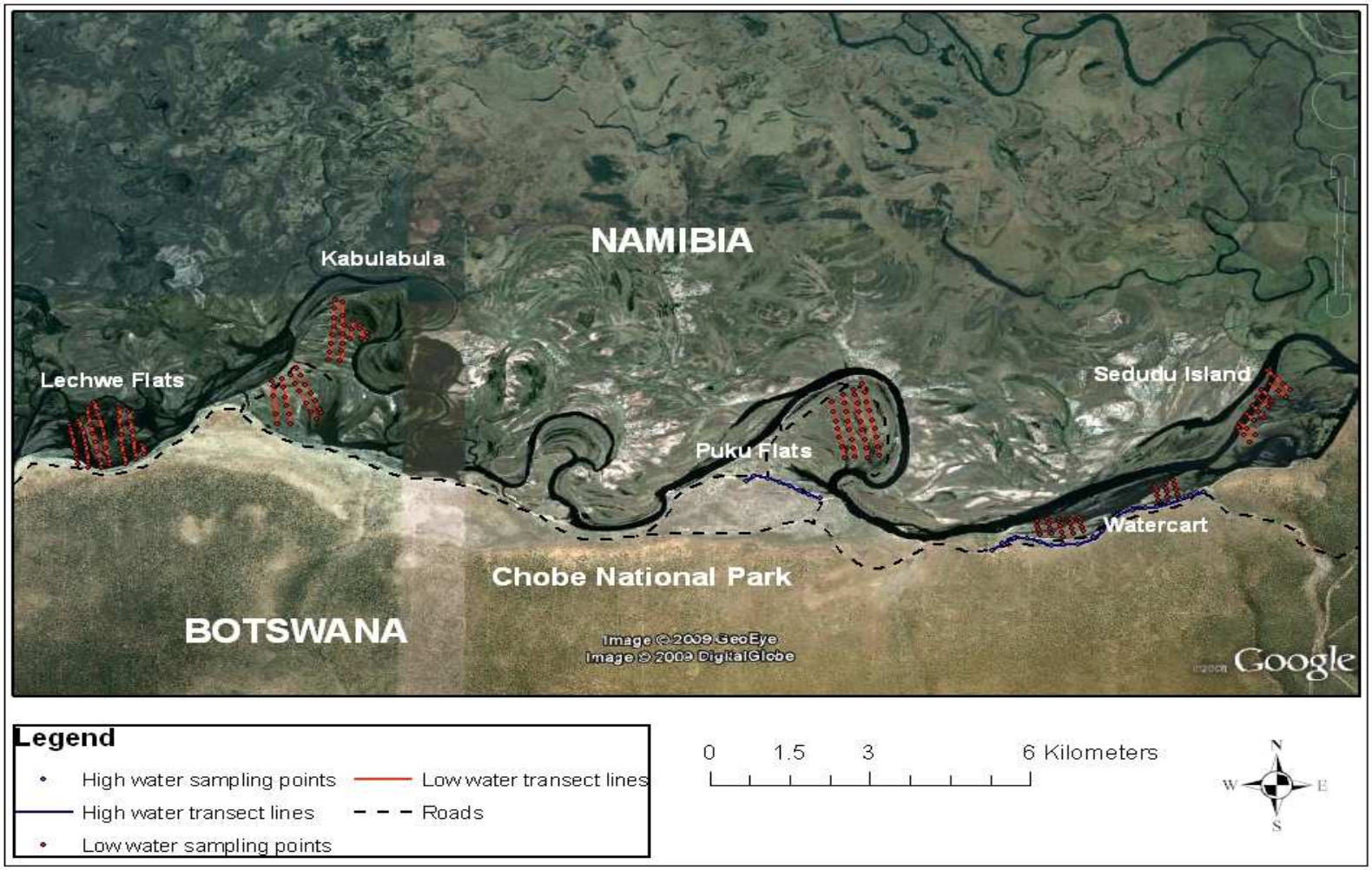

Figure 24: Locations of the sampling transects during the LWS and HWS along with the additional transects sampled during the HWS.

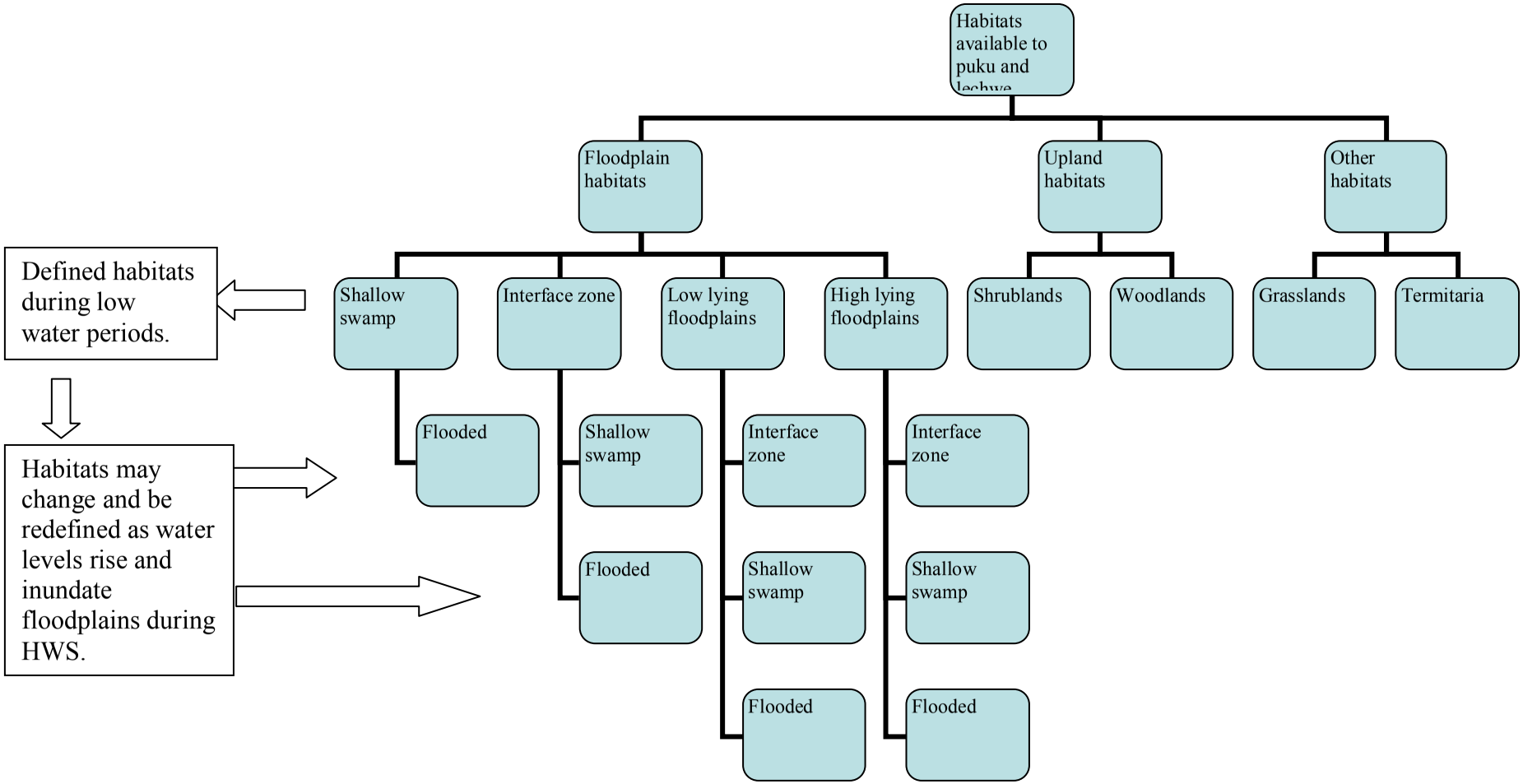

Figure 25: Flow chart depicting how habitat classifications may change as flood waters rise along the Chobe River floodplains.

Table 3: Results of the forward stepwise logistic regression for the low water season.

		Hosmer and Lemeshow Test			Pearson Test			Classification (cut value is 0.500)		
Species	**Model**	**Chi-square**	**df**	***P***	**Chi-square**	**df**	***P***	**Specificity**	**Sensitivity**	**Overall Correct Prediction**
Puku	1	13.011	8	0.111	17.546	1	0.000	93.5	23.7	69.5
	2	14.848	8	0.062	15.889	1	0.000	90.8	32.0	70.6
	3	6.863	8	0.552	7.436	1	0.006	90.8	32.0	70.6
	4	**7.883**	**8**	**0.445**	**16.994**	**5**	**0.005**	**88.6**	**44.3**	**73.4**
	5	9.735	8	0.284	4.502	1	0.034	89.7	45.4	74.5
	6	7.321	8	0.502	6.181	1	0.013	88.6	47.4	74.5
	7	9.379	8	0.311	3.021	1	0.082	88.1	49.5	74.8
	8	6.236	8	0.621	2.976	1	0.085	89.7	52.6	77.0
Lechwe	1	0.006	4	1	62.577	5	0.000	96.8	32.6	76.4
	2	**8.044**	**8**	**0.429**	**39.659**	**1**	**0.000**	**94.1**	**54.7**	**81.6**
	3	7.659	8	0.467	11.376	1	0.001	91.9	51.2	79.0
	4	16.129	8	0.041	7.679	1	0.006	93.0	59.3	82.3
	5	11.191	8	0.191	3.131	1	0.077	94.1	60.5	83.4
	6	22.999	8	0.003	3.398	1	0.065	94.1	67.4	85.6

			Variables in the Equation							
Species	**Model**	**Variable**	**B**	**S.E.**	**Wald**	**df**	***P***	**Odds ratio**	**90% C.I. for Odds ratio**	
									Lower	**Upper**
Puku	4	**Shallow swamp**			**11.72**	**5**	**0.039**			
		Interface zone	**2.59**	**1.19**	**4.71**	**1**	**0.030**	**13.279**	**1.29**	**137.1**
		Low lying flood.	1.18	1.08	1.18	1	0.278	3.24	0.39	27.13
		High lying flood.	1.34	1.1	1.49	1	0.222	3.809	0.44	32.64
		Grasslands	**2.5**	**1.21**	**4.26**	**1**	**0.039**	**12.187**	**1.13**	**130.9**
		Shrublands	-4.78	12.39	0.15	1	0.700	0.008	0.00	2.94E+08
		Grass height	**0.00**	**0.00**	**6.89**	**1**	**0.009**	**0.998**	**0.996**	**0.999**
		Grass cover	**0.04**	**0.01**	**24.14**	**1**	**0.000**	**1.041**	**1.02**	**1.06**
		Grass green.	**-0.06**	**0.02**	**11.47**	**1**	**0.001**	**0.943**	**0.91**	**0.98**
		Constant	0.18	1.75	0.01	1	0.919	1.196		
Lechwe	2	**Shallow swamp**			**40.42**	**5**	**0.000**			
		Interface zone	**2.047**	**0.693**	**8.714**	**1**	**0.003**	**7.745**	**1.989**	**30.148**
		Low lying flood	**-1.112**	**0.513**	**4.701**	**1**	**0.03**	**0.329**	**0.12**	**0.899**
		High lying flood	**-1.152**	**0.555**	**4.313**	**1**	**0.038**	**0.316**	**0.107**	**0.937**
		Grasslands	**1.958**	**0.784**	**6.24**	**1**	**0.012**	**7.086**	**1.525**	**32.935**
		Shrublands	-4.842	12.817	0.143	1	0.706	0.008	0.000	6.41E+08
		Grass cover	**0.057**	**0.01**	**30.254**	**1**	**0.000**	**1.059**	**1.037**	**1.08**
		Constant	-4.3	0.871	24.358	1	0.000	0.014		

Table 4: Results of the forward stepwise logistic regression for the high water season.

		Hosmer and Lemeshow Test			Pearson Test			Classification (cut value is 0.500)		
Species	**Model**	**Chi-square**	**df**	***P.***	**Chi-square**	**df**	***P.***	**Specificity**	**Sensitivity**	**Overall Correct Prediction**
Puku	1	0.003	3	1.000	42.392	7	0.000	24.5	100	71.8
	2	23.174	8	0.003	20.429	1	0.000	64.2	88.8	79.6
	3	1.889	8	0.984	12.752	1	0.000	67.9	88.8	80.9
	4	5.030	8	0.754	28.292	1	0.000	79.3	89.9	85.9
	5	**1.974**	**8**	**0.982**	**6.290**	**1**	**0.012**	**83.0**	**92.1**	**88.7**
Lechwe	**1**	**1.608**	**6**	**0.952**	**77.846**	**1**	**0.000**	**100**	**87.879**	**95.4**
	2	15.722	8	0.047	23.138	1	0.000	100	93.939	97.7
	3	0.819	8	0.999	2.905	1	0.088	100	96.970	98.8

			Variables in the Equation							
Species	**Model**	**Variable**	**B**	**S.E.**	**Wald**	**df**	***P.***	**Odds ratio**	**90% C.I. for Odds ratio**	
									Lower	**Upper**
Puku	5	Shallow swamp			2.872	7	0.897			
		Interface zone	11.564	41.230	0.079	1	0.779	1.053E+05	0.000	1.309E+40
		Low lying flood.	17.639	81.645	0.047	1	0.829	4.578E+07	0.000	1.437E+77
		High lying flood.	9.619	41.220	0.054	1	0.815	1.505E+04	0.000	1.836E+39
		Grasslands	19.539	60.339	0.105	1	0.746	3.061E+08	0.000	7.028E+59
		Shrublands	10.816	41.222	0.069	1	0.793	4.980E+04	0.000	6.105E+39
		Woodlands	-6.982	183.323	0.001	1	0.970	0.001	0.000	1.031E+153
		Termitaria	17.447	169.353	0.011	1	0.918	3.778E+07	0.000	5.385E+151
		Distance to water	**0.025**	**0.007**	**13.737**	**1**	**0.000**	**1.025**	**1.012**	**1.039**
		Grass height	**-0.006**	**0.002**	**11.443**	**1**	**0.001**	**0.994**	**0.990**	**0.997**
		Grass cover	**0.059**	**0.018**	**10.950**	**1**	**0.001**	**1.061**	**1.024**	**1.098**
		Grass green.	**0.049**	**0.021**	**5.130**	**1**	**0.024**	**1.050**	**1.007**	**1.095**
		Constant	-15.157	41.245	0.135	1	0.713	0.000		
Lechwe	1	**Grass green.**	**0.312**	**0.077**	**16.288**	**1**	**0.000**	**1.366**	**1.174**	**1.589**
		Constant	-22.465	5.520	16.560	1	0.000	0.000		

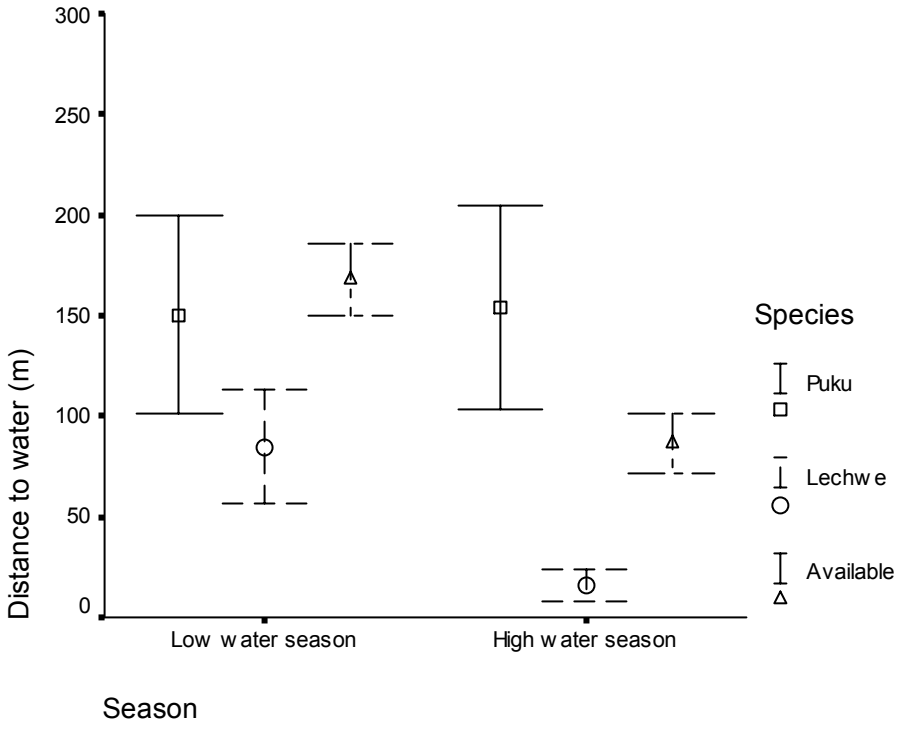

Figure 26: Seasonal mean distance to water of puku and lechwe foraging sites, compared to availability. Bars represent 95% confidence intervals.

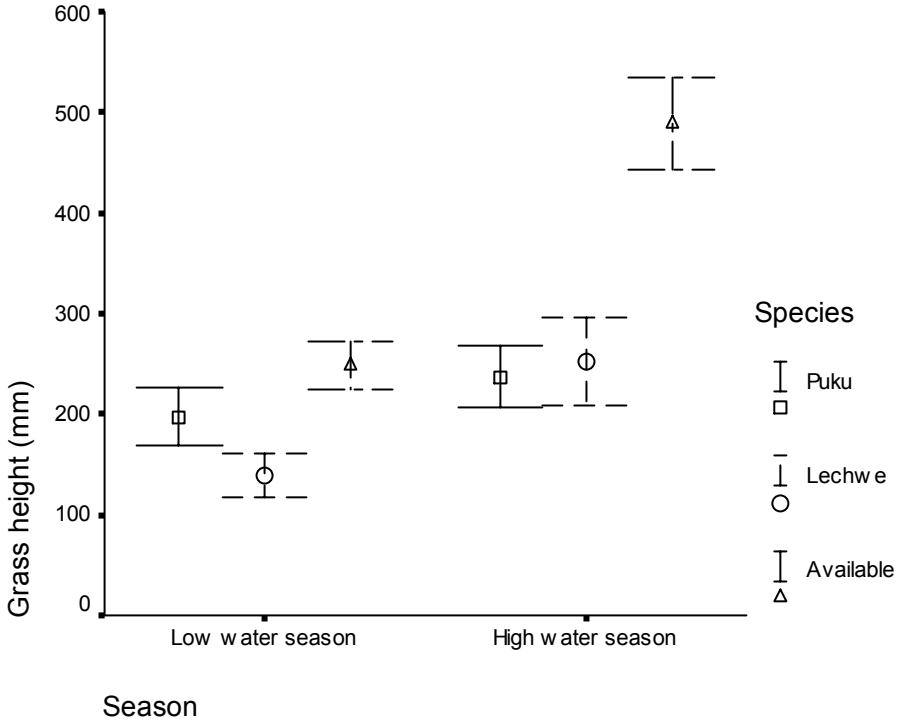

Figure 27: Seasonal mean grass height at puku and lechwe foraging sites, compared to availability. Bars represent 95% confidence intervals.

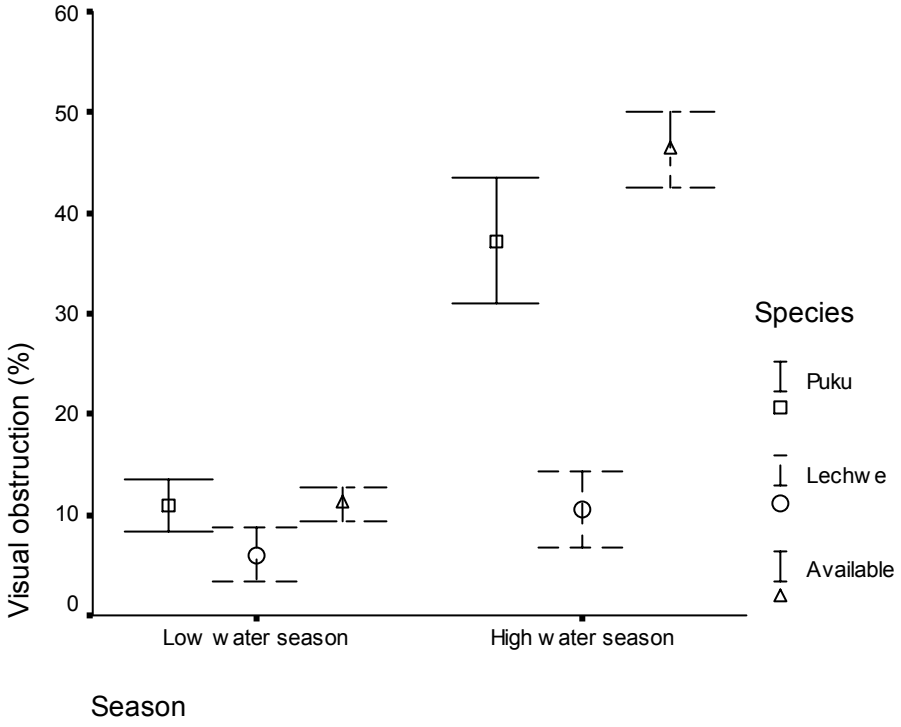

Figure 28: Seasonal mean visual obstruction at puku and lechwe foraging sites, compared to availability. Bars represent 95% confidence intervals.

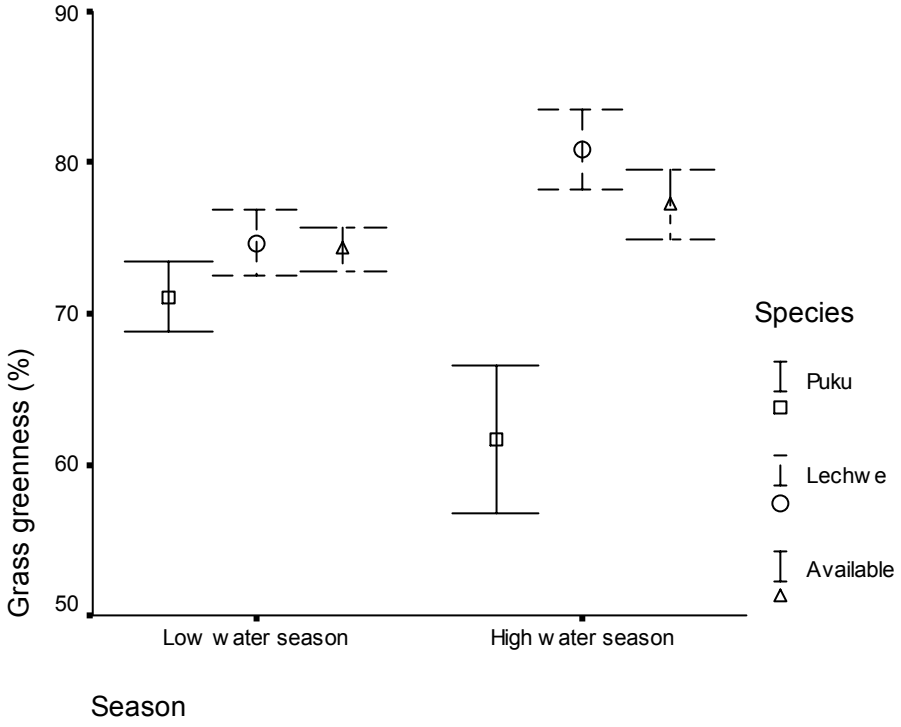

Figure 29: Seasonal mean grass greenness at puku and lechwe foraging sites, compared to availability. Bars represent 95% confidence intervals.

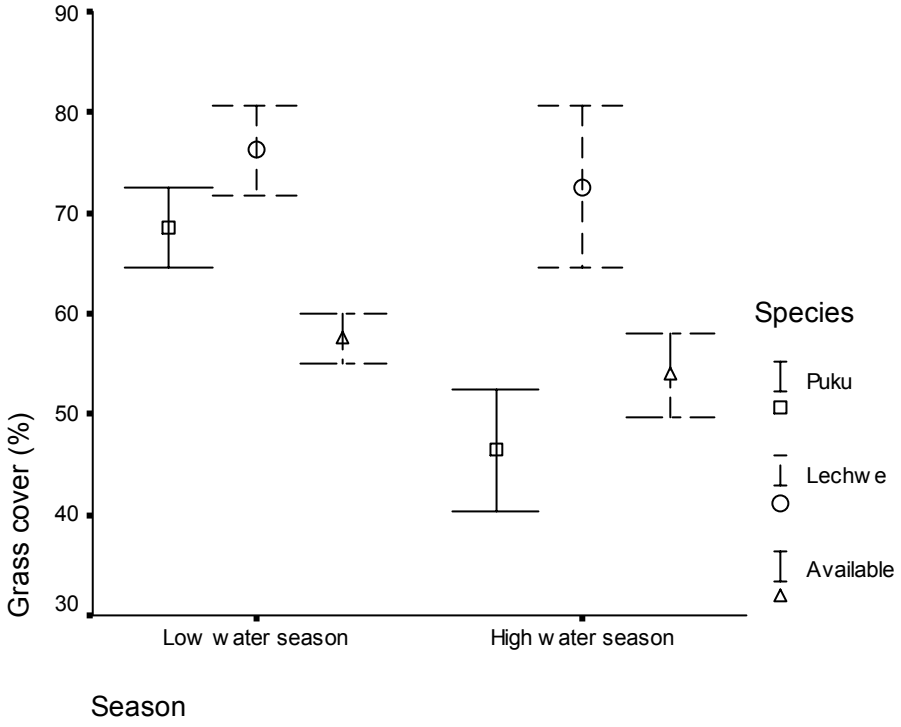

Figure 30: Seasonal mean grass cover at puku and lechwe foraging sites, compared to availability. Bars represent 95% confidence intervals.

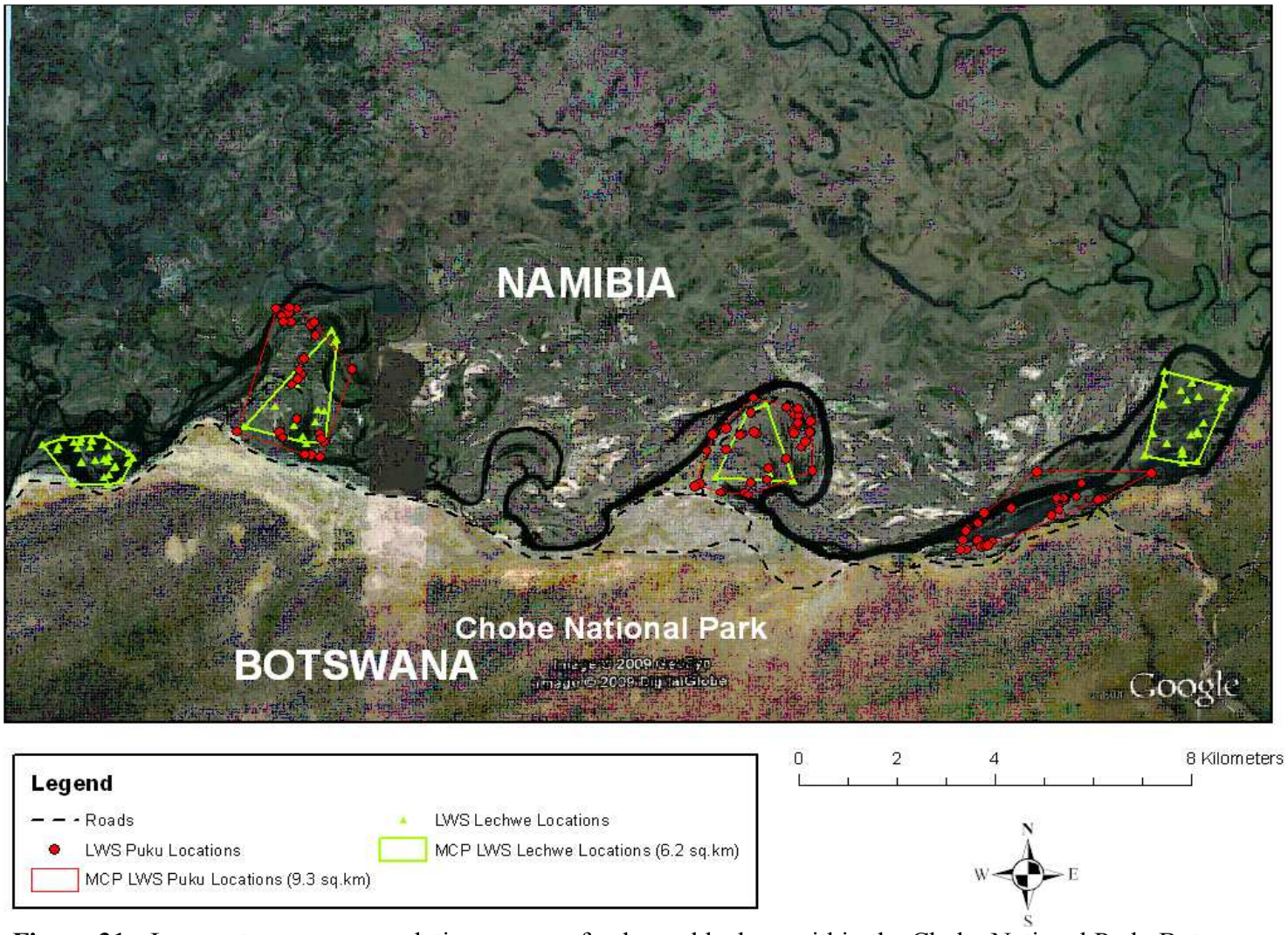

Figure 31: Low water season population ranges of puku and lechwe within the Chobe National Park, Botswana.

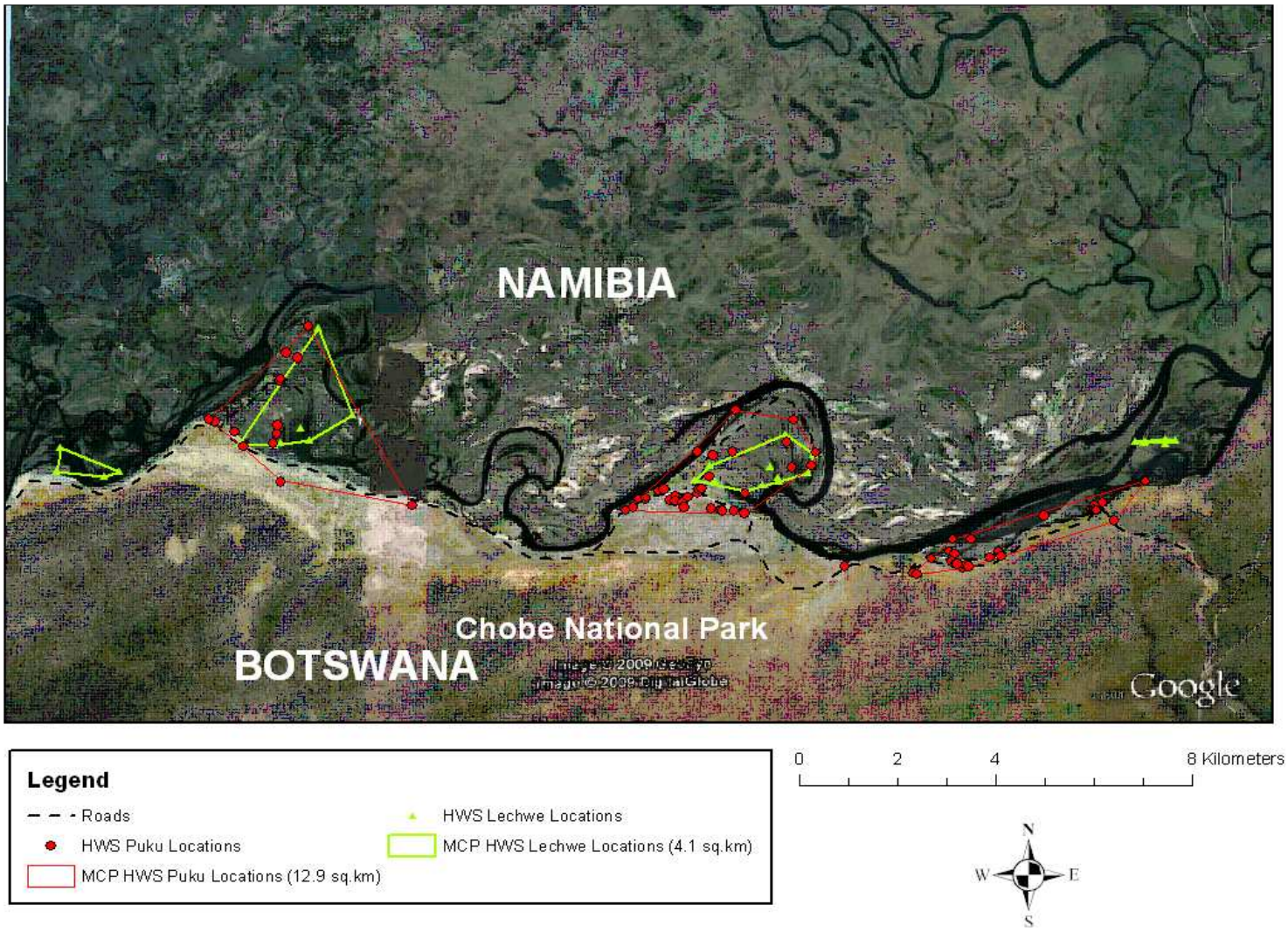

Figure 32: High water season population ranges of puku and lechwe within the Chobe National Park, Botswana.

References

Abramsky, Z., Rosenzweig, M.L. & Subach, A., (2002), *The costs of apprehensive foraging,* Ecology, 83:1330-1340.

Alden, P.C., Estes, R.D., Schlitter, D. & McBride, B., (1995), *National Audubon Society Field Guide to African Wildlife*, New York: Chanticleer Press.

Allen, L.D.C., (1963), *The lechwe of the Bangweulu swamps,* Puku, 1: 1-8.

ArcMap, version 9.0, ESRI, 380 New York Street, Redlands, California.

Arnold, G.W. & Dudzinski, M.L. (1963), *The use of faecal nitrogen as an index for estimating the consumption of herbage by grazing animals,* The Journal of Agricultural Science, 61: 33-43.

ARC Institute for Soil, Climate and Water Laboratory, Pretoria, South Africa.

Bartolome, J., Franch, J., Plaixats, J., & Seligman, N.G., (1998), *Diet selection by sheep and goat on Mediterranean hearth-woodland range,* Journal of Range Management, 51:383-391.

Baumont, R., Prache, S., Meuret, M. & Morand-Fer, P., (2004), *Measurement of herbage intake and ingestive behaviour by housed animals,* In: Herbage Intake Handbook, 2nd Edition, (Ed. P.D. Penning), The British Grassland Society, Reading UK, p.121-149.

Bearden, H.J. & Fuquay, J.W., (1992), *Nutritional management. In: Applied animal reproduction,* Prentice Hall, Englewood Cliffs, New Jersey, pp 283-292.

Bell, R.H., (1970), *The use of the herb layer by grazing ungulates in the Serengeti*. In: *Animal Populations in Relation to Their Food Resources* (eds: A. Watson). Blackwell Scientific Publications, Oxford pp. 112-124.

Bell, R.H., (1971), *A grazing ecosystem in the Serengeti,* The Scientific American, 4: 86-93.

Bell, R.H., (1982), *The effect of soil nutrient availability on community structure in African ecosystems,* In: Ecology of Tropical Savannas, Eds., B.J. Huntley & B.H. Walker, Springer-Verlag, New York.

Bell, R.H., (1984), *Soil-plant-herbivore interactions,* In: Conservation and wildlife management in Africa, (Eds. Bell, R.H.V., & McShane-Caluzi, E.), U.S. Peace Corps, Washington D.C., p.59-84.

Belonje, P.C., (1980), *The use of faecal samples to estimate the phosphorus intake by grazing sheep, 1, The use of pool instead of individual samples,* The Onderstepoort Journal of Veterinary Research, 47: 163-167.

Ben-Shahar, R., (1996), *Woodland dynamics under the influence of elephants and fire in northern Botswana,* Vegetatio, 123: 153-163.

Ben-Shahar, R., & Coe, M.J., (1992), *The relationships between soil factors, grass nutrients and the foraging behaviour of wildebeest and zebra,* Oecologia, 90(3): 422-428.

Ben-Shahar, R., & MacDonald, D.W., (2002), *The role of soil factors and leaf protein in the utilization of mopane plants by elephants in northern Botswana,* BMC Ecology, 2(3): 1-6.

Bendel, R.B. & Afifi, A.A., (1977), *Comparison of stopping rules in forward stepwise regression,* Journal of the American Statistical Association, 72: 46-53.

Berry, H. H. & Louw, G.N. (1982), *Nutritional measurements in a population of free-ranging wildebeest in the Etosha National Park,* Madoqua, 13:101-125.

Bertram, R.R., (1978), *Living in groups: predators and prey. In: Behavioural Ecology: an Evolutionary Approach,* (Eds. J.R. Krebs & N.B. Davies) Blackwell Scientific Publications, Oxford.

Bombay, H.L., Morrison, M.L., & Hall, L.S., (2003), *Scale perspectives in habitat selection and animal performance for willow flycatchers in the central Sierra Nevada, California,* Studies in Avian Biology, 26: 60-72.

Bowyer, R.T., Kie, J.G. & Van Ballenberghe, V., (1998), *Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation?* Journal of Mammalogy, 79: 415-425.

Brand, M.R., (1978), *A method to correct for differential digestibility in fecal analysis,* American Midland Naturalist, 100(1): 228-232.

Brown, J.H., (1984), *On the relationship between abundance and distribution of species,* The American Naturalist, 124: 255-277

Bryant, J.P., Kuropat, P.J., Cooper, S.M., Frisby, K., & Owen-Smith, N., (1989), *Resource availability hypothesis of plant antiherbivore defense tested in a South African savanna ecosystem,* Nature, 340: 227-229.

Campbell, A, (1990), *The nature of Botswana,* In: A guide to conservation and development (Middleton, N. & Bilboae, S.A.) IUCN, Spain.

Chacon, E. & Stobbs, T.H., (1976), *Influence of progressive defoliation of a grass sward on the eating behaviour of cattle,* Australian Journal of Agricultural Research, 27(5): 709-727.

Child, G., (1968), *Report to the government of Botswana on an ecological survey of north-eastern Botswana,* FAO Rome: 155pp.

Child, G. & Von Richter, W., (1969), *Observations on ecology and behaviour of lechwe, puku and waterbuck along the Chobe River, Botswana,* Saugetierk, 34: 275-295.

Church, D.C., (1969), *Digestive physiology and nutrition of ruminants.* Vol I. Digestive physiology, Oregon State University, Corvallis, Pp. 316.

Cook, J.G., Irwin, L.L., Bryant, L.D. & Thomas, J.W., (1994), *Faecal nitrogen and dietary quality relationships in juvenile elk,* Journal of Wildlife Management, 58(1): 46-53.

Costanza, M.E. & Afifi, A.A., (1979), *Comparison of stopping rules in forward stepwise discriminant analysis*, Journal of the American Statistical Association, 74: 777–785.

De Vos, A. & Dowsett, R.J., (1966), *The behaviour and population structure of three species in the genus Kobus,* Mammalia, 30: 30-35.

Department of Meteorological Services, Ministry of Environment, Wildlife and Tourism, P.O. Box 10100, Gaborone, Botswana, (2007).

Diposto, F.M. & Skarpe, C. (2006), *Population status and distribution of puku in a changing riverfront habitat in northern Botswana,* South African Journal of Wildlife Research, 36(1):89-97.

Duncan, P., (1975), *Topi and Their Food Supply*, PhD Thesis, University of Nairobi.

Dye, P.J. & Walker, B.H., (1987), *Patterns of shoot growth in a semi-arid grassland in Zimbabwe,* The Journal of Applied Ecology, 24 (2): 633-644.

East, R., (1989), *Antelopes global survey and regional action plans, Part 2: Southern and south-central Africa.* IUCN/SSC Antelope Specialist Group.

Fenn, M.G.P. & Macdonald, D.W., (1995), *Use of middens by red foxes: Risk reverses rhythms of rats,* Journal of Mammology, 76:130-136.

Ferguson, S. H., Bergerud, A.T. & Ferguson, R., (1988), *Predation risk and habitat selection in the persistence of a remnant caribou population,* Oecologia, 76: 236-245.

Fischer, F., & Linsenmair, K.E., (2001), *Spatial and temporal habitat use of kob antelopes in the Comoé National Park, Ivory Coast, as revealed by radio tracking,* African Journal of Ecology, 39: 249-256.

Frank, D.A., McNaughton, S.J. & Tracey, B.F., (1998), *The ecology of the earths grazing ecosystems,* Bioscience, 48(7): 513-521.

Frank, D.A., (2008), *Ungulate and topographic control of nitrogen: phosphorus stoichiometry in a temperate grassland; soils, plants and mineralization rates,* Oikos, 117: 591-601.

Fretwell, S.D. & Lucas, H.L. Jr, (1969), *On territorial behavior and other factors influencing habitat distribution in birds,* Acta Biotheoretica, 14:16-36.

Fritz, H., Wichatitsky, M.D. & Letessier, G., (1996), *Habitat use by sympatric wild and domestic herbivores in an African savanna woodland: the influence of cattle spatial behaviour,* Journal of Applied Ecology, 33: 589-598.

Fryxell, J.M. & Sinclair, A.R.E., (1988), *Causes and consequences of migration by large herbivores,* Trends in Ecology and Evolution, 3(9): 237-241.

Fryxell, J.M., Wilmshurst, J.F. & Sinclair, A.R.E., (2004), *Predictive models of movement by Serengeti grazers,* Ecology 85:2429-2435.

Gammon, D.M. & Roberts, B.R., (1978), *Patterns of defoliation during continuous and rotational grazing of the Matopos Sandveld of Rhodesia*, Rhodesian Journal of Agricultural Research, 16: 117-131.

Garson, G.D., (2009), *Testing of assumptions,* Statistical notes from the North Carolina State University.

Gates, C.C. & Hudson, R.J., (1981), *Habitat selection by wapiti in a boreal forest enclosure,* Naturaliste Can. (Rev. Ecol. Syst.), 108: 153-166.

Geist, V., (1974), *On the relationship of social evolution and ecology in ungulates,* American Zoologist, 14: 205-220

Georgiadis, N.J. & McNaughton, S.J., (1990), *Elemental and fibre contents of savannah grasses: Variation with grazing, soil type, season, and species,* The Journal of Applied Ecology, 27 (2): 623-634.

Gilliam, J.F. & Fraser, D.F., (1987), *Habitat selection when foraging under predation hazard: a model and a test with stream-dwelling minnows*, Ecology, 68: 1856–1862.

Goldspink, C.K., Holland, R.K., Sweet, G. & Sjernstedt, R., (1998), *A note on the distribution and abundance of puku, Kobus vardonii Livingstone, in Kasanka National Park, Zambia,* African Journal of Ecology, 36: 23-33.

Gosling, L.M., (1986), *The evolution of male mating strategies in antelopes,* In: Ecological aspects of social evolution: Birds and Mammals (Eds. Rubenstein, D.I. & Wrangham, R.W.), Princeton, Princeton University Press, p.241-281.

Gosling, L.M. & Petrie, M., (1990), *Lekking in topi: a consequence of satellite behaviour by small males at hotspots,* Animal Behaviour, 40: 272-287.

Grant, C.C., Meissner, H.H., & Schultheiss, W.A., (1995), *The nutritive value of veld as indicated by faecal phosphorus and nitrogen and its relation to the condition and movement of prominent ruminants during the 1992-1993 drought in the Kruger National Park,* Koedoe, 38: 17-31.

Grassman, B.T. & Hellgren, E.C., (1993), *Phosphorus nutrition in white-tailed deer: nutrient balance, physiological responses, and antler growth,* Ecology, 74(8): 2279-2296.

Grobler, J.H., (1981), *Feeding behaviour of sable Hippotragus niger niger (Harris 1838) in the Rhodes Matopos National Park, Zimbabwe,* South African Journal of Wildlife Research, 16: 50-58.

Grzimek, M. & Grzimek, B., (1960), *A study of the game of the Serengeti Plains*, Z. für Saügetierk, 25: 1–61.

Hamilton, W.D., (1971), *Geometry of the selfish herd,* Journal of Theoretical Biology, 31: 295-311.

Hansen, R.M., & Reid, L.D., (1975), *Diet overlap of deer, elk, and cattle in southern Colorado,* Journal of Range Management, 28(1): 43-47.

Harestadt, A.S. & Bunnel, F.L., (1979), *Home range and body weight – a re-evaluation,* Ecology, 60: 389-402.

Harrington, R., Owen-Smith, N., Viljoen, P.C. Biggs, H.C., Mason, D. & Funston, P., (1999), *Establishing the causes of the roan population decline in the Kruger National Park, South Africa,* Biological Conservation, 90: 69 – 78

Hoffman, R. R. & Stewart, D.R.M., (1972), *Grazer or browser: A classification based on the stomach structure and feeding habits of east African ruminants,* Mammalia, 36: 226-240.

Hoffman, R.R., (1973), *The ruminant stomach,* East African Monographs in Biology, 2: 1-354.

Holechek, J.L., Vavra, M., & Pieper, R.D., (1982), *Botanical composition determination of range herbivore diets. A review,* Journal of Range Management 35(3): 309-315.

Hosmer, D.W. & Lemeshow, S., (2000), *Applied logistic regression,* 2nd Edition, John Wiley & Sons Inc, Hoboken, New Jersey.

Hughes, F.M.R., (1988), *The ecology of African floodplain forests in semi-arid and arid zones: A review,* Journal of Biogeography, 15(1): 127-140.

Illius, A.W., Gordon, I.J., Elston, D.A. & Milne, J.D., (1999), *Diet selection in goats: A test of intake-rate maximization,* Ecology, 80(3): 1008-1018.

Jarman, P.J., (1974), *The social organization of antelope in relation to their ecology,* Behaviour, 48(3/4): 215-267.

Jenks, J.A., Leslie, D.M., Lochmiller, R.L., Melchiors, M.A. & Warde, W.D., (1989), *Effect of compositing samples on analyses of fecal nitrogen,* The Journal of Wildlife Management, 53(1): 213-215.

Jones, E.C., (1971), *Grassland ecology,* (Ed. By C.R.W Spedding), Oxford University Press, London, p.86.

Ketelaars, J.J.M.H., (1986), *Prediction of feeding intake,* In: Modeling of extensive livestock production systems, Edited by N. de Ridder, H. van Keulen, N.G. Seligman, & P.J.H. Neate, p.108-161. Addis Ababa: International Livestock Centre for Africa.

Kingdon, J., (1997), *The Kingdon field guide to African mammals,* Academic Press, London, 1997.

Klop, E., & Van Goethem, J., (2008), *Savanna fires govern community structure of ungulates in Běnouě National Park, Cameroon,* Journal of Tropical Ecology, 24: 39-47.

Knoop, M.C. & Owen-Smith (2006), *Foraging ecology of roan antelope. Key resources during critical periods,* African Journal of Ecology, 44: 228-236.

Knoop, M.C. & Owen-Smith, N., (2006), *Foraging ecology of roan antelope: key resources during critical periods,* African Journal of Ecology, 44(2): 228-236.

Lacher, T.E., Willig, M.R. & Mares, M.A., (1982), *Food preference as a function of resource abundance with multiple prey types: An experimental analysis of optimal foraging theory,* The American Naturalist, 120(3): 297-316.

Lancaster, R.J., (1949), *The measurement of food intake by grazing cattle and sheep. A method of calculating the digestibility of pasture based on the nitrogen content of faeces derived from the pasture.*

Laver, P., (2005), *Kernal home range estimation for ArcGIS, using VBA and ArcObjects,* Abode user manual, Virginia Tech University.

Lee, K.I. & Koval, J.J., (1997), *Determination of the best significance level in forward stepwise logistic regression,* Communications in Statistics – Simulations, 26: 559-575.

Lent, P.C., (1969), *A preliminary study of the Okavango lechwe,* East African Wildlife Journal, 7: 147-157.

Leslie, D.M., Vavra, M., Starkey, E.E., & Slater, R.C., (1983), *Correcting for differential digestibility in microhistological analyses involving common coastal forages of the Pacific north-west,* Journal of Range Management, 36(6): 730-732.

Leslie, D.M. & Starkey, E.E., (1985), *Fecal indices to dietary quality of cervids in old-growth forests,* The Journal of Wildlife Management, 49(1): 142-146.

Liversidge, R. & Berry, M.P.S., (1995), *Voeding*, In: Bothma, J. du P. (ed). Wildplaasbestuur, Van Schaik, Pretoria.

Livingstone, D., (1857), *Missionary travels and researches in South Africa,* W. Clowes & Sons, Stanford Street, London, 1857.

Macandza, V.A., Owen-Smith, N, & Cross, P.C., (2004), *Forage selection by African buffalo in the late dry season in two landscapes,* South African Journal of Wildlife Research, 34(2): 113-121.

Magome, H., Cain, J.W., Owen-Smith, N., & Henley, S.R., (2008), *Forage selection of sable antelope in Pilanesberg Game Reserve, South Africa,* South African Journal of Wildlife Research, 38(1): 35-41.

Mangel, M. & Clark, C.W., (1986), *Towards a unified foraging theory,* Ecology, 67(5): 1127-1138.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., & Erickson, W.P., (2002), *Resource selection by animals: Statistical design and analyses for field studies,* 2nd Edition, Kluwer Academic Publisher, London.

Mao, J.S., Boyce, M.S., Smith, D.W., Singer, F.J., Vales, D.J., Vore, J.M. & Merrill, E.H., (2005), *Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park,* The Journal of Wildlife Management, 69(4): 1691-1707.

McInnes, M.L., Vavra, M. & Krueger, W.C., (1983), *A comparison of four methods used to determine the diets of large herbivores,* Journal of Range Management, 36: 302-306.

McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E., & Contasti, A.L., (2010), *Considering ecological dynamics in resource selection functions,* Journal of Animal Ecology, 79:4-12.

McNab, B.K., (1963), *Bioenergetics and the determination of home range size,* American Naturalist, 97: 133-140.

McNaughton, S.J., (1979), *Grazing as an optimization process: grass-ungulates relationships in the Serengeti,* American Naturalist, 113: 691-703.

McNaughton, S.J., (1990), *Mineral nutrition and seasonal movements of African migratory ungulates,* Nature, 14: 613-615.

McNaughton, S.J. & Georgiadis, N.J., (1986), *Ecology of African grazing and browsing mammals,* Annual Review of Ecology and Systematics, 17: 39-66.

Mduma & Sinclair, (1994), *The function of habitat selection by oribi in Serengeti, Tanzania,* African Journal of Ecology 32(1): 16-29.

Mech, L.D., (1977), *Wolf-pack buffer zones as prey reservoirs,* Science, 198:320-321.

Mickey, R.M. & Greenland, S., (1989), *The impact of confounder selection criteria on effect estimation,* American Journal of Epidemiology, 129(1): 125-137.

Mills, M.G.L. & Hes, L., (1997), *The complete book of southern African mammals,* Struik Publishers, Cape Town 8001.

Mills, M.G.L. & Shenk, T.M., (1992), *Predator-Prey relationships: The impacts of lion predation on wildebeest and zebra populations,* The Journal of Animal Ecology, 61(3): 693-702.

Modha, K.L. & Eltringham, S.K., (1976), *Population ecology of the Uganda kob in relation to the territorial system in the Rwenzori National Park, Uganda,* The Journal of Applied Ecology, 13(2): 453-473.

Moir, K.W., (1960), *Nutrition of grazing cattle, 1, Estimation of protein in pasture selected by grazing cattle,* Queensland Journal of Agricultural Science, 17: 361-371.

Morris, D.W., (2003), *Towards an ecological synthesis: A case for habitat selection,* Oecologia, 136:1-13.

Mosugelo, D.K., Moe, S.R., Ringrose, S., & Nellemann, C., (2002), *Vegetation changes during a 36-year period in northern Chobe National Park, Botswana,* African Journal of Ecology 40(3): 232-240.

Mysterud, A., (2000), *Diet overlap among ruminants in Fennoscandia,* Oecologia, 124(1): 130-137.

Neu, C., Byers, C. & Peek, J., (1974), *A technique for analysis of utilization-availability data,* Journal of Wildlife Management, 38: 541-545.

Nowak, R.M., (1991), *Walker's Mammals of the World*, Fifth Edition, Baltimore: The Johns Hopkins University Press.

Owen-Smith, N., (1982), *Factors influencing the consumption of plant products by large herbivores,* In: Huntley, B.J. & Walker, B.H., editors. The ecology of tropical savannas, Springer-Verlag, Berlin, Germany, p. 359-404.

Owen-Smith, N., (1994), *Foraging responses of kudus to seasonal changes in food resources: Elasticity in constraints,* Ecology, 75(4): 1050-1062.

Owen-Smith, N. (2002), *A metaphysiological modeling approach to stability in herbivore – vegetation systems,* Ecological modeling, 149: 153-178.

Owen-Smith, N., (2005), *Adaptive herbivore ecology: From resources to populations in variable environments,* Student Edition, Wits University Press, Johannesburg, South Africa.

Owen-Smith, N. & Cooper, S.M., (1987), *Assessing food preferences of ungulates by acceptability indices,* Journal of Wildlife Management, 51: 372-378.

Owen-Smith, N. & Novellie, P., (1982), *What should a clever ungulate eat?* The American Naturalist, 119(2): 151-178.

O'Reagain, P.J., (2001), *Foraging strategies on rangeland: effects on intake and animal performance,* XIX International Grassland Congress.

O'Shaughnessy, R., (2006, unpublished), *The relationship between dry season grass species selection and faecal nutrients of sable antelope in two regions of the Kruger National Park,* Honours Research Report, University of the Witwatersrand, Johannesburg.

Parsons, A.J., Thornley, J.H.M., Newman, J. & Penning, P.D., (1994), *A mechanistic model of some physical determinants of intake rate and diet selection in a two-species temperate grassland sward,* Functional Ecology 8(2): 187-204.

Pianka, E.R., (1973), *The structure of lizard communities,* Annual Review of Ecology and Systematics, 4: 53-74.

Pulliam, D.E. & Nelson, J.R., (1979), *Determination of digestibility coefficients for quantification of fecal analysis with elk,* In: North American Elk: Ecology, Behaviour

and Management, Eds., M.S. Boyce & L.D. Hayden-Wing, University of Wyoming, Laramie, p.240-246.

Pulliam, H.R., (1989), *Individual behaviour and procuring essential resources,* In: Perspectives in ecological theory, (Eds. May, R.M. & Levin, S.A.), Princeton University Press, Princeton, New Jersey, p.25-38.

Rees, W.A., (1978[a]), *The Ecology of the Kafue lechwe: Soils, water levels and vegetation,* The Journal of Applied Ecology, 15(1): 163-176.

Rees, W.A., (1978[b]), *The ecology of the Kafue lechwe: The food supply,* The Journal of Applied Ecology, 15(1): 177-191.

Rettie, W.J. & Messier, F., (2000), *Hierarchical habitat selection by woodland caribou: its relationship to limiting factors,* Ecography, 23: 466-478.

Ripple, W.J., & Beschta, R.L., (2004), *Wolves and the ecology of fear: can predation risk structure ecosystems?* Bioscience, 54:755-766.

Robbins, C.T., (1983), *Wildlife feeding and nutrition,* Academic Press, New York.

Robinette, W.L. & Child, G.F.T., (1964), *Notes on biology of the lechwe,* Puku, 2: 84-117.

Rosenzweig, M.L., (1981), *A theory of habitat selection,* Ecology, 62:327-335.

Ross, K., Thouless, C., Gibson, D., Masogo, R., & Dooley, B., (1998), *Botswana,* In: Antelope survey update, Number 7, January 1998 (Compiled by East, R.), IUCN/SSC Antelope Specialist Group, Gland.

Rutina, L.P., Du Toit, J.T., Moe, S.R., & Hytteborn, H., (2004), *Browsing ungulates limit tree seedling survival in the Chobe riparian zone, northern Botswana,* In: Rutina, L.P., Impalas in an elephant impacted woodland: browser-driven dynamics of the Chobe riparian zone, northern Botswana, Ph.D. thesis, 2004: 8, Agricultural University of Norway, Ås.

Sale, P.F., (1974), *Overlap in resource use, and interspecific competition,* Oecologia 17: 245-256.

Sanders, K.D., Dahl, B.E., & Scott, G., (1980), *Bite-count vs fecal analyses for range animal diets,* Journal of Range Management, 33(2): 146-149.

Schoener, T.W. (1974), *Resource partitioning in ecological communities,* Science, 185 (4145): 27-39.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., & Gitzen, R.A., (1999), *Effects of Sample Size on Kernel Home Range Estimates*, Journal of Wildlife Management, 63(2): 739-747.

Senft, R.L., Coughnour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. (1987), *Large herbivore foraging and ecological hierarchies – landscape ecology can enhance traditional foraging theory,* BioScience, 37: 789-799.

Sheppe, W. & Osbourne, T., (1971), *Patterns of use of a floodplain by Zambian mammals,* Ecological Monographs, 41(3): 179-205.

Simpson, C.D., (1975), *A detailed vegetation study on the Chobe River in north-eastern Botswana,* Kirkia, 10: 185-227.

Simpson, C.D., (1978), *Effects of elephant and other wildlife on vegetation along the Chobe River, Botswana,* Occasional papers of the Museum of Texas Tech University, 48: 1-15.

Sinclair, A.R.E., (1970), *Studies in the ecology of the east African buffalo,* Ph.D. thesis, University of Oxford.

Sinclair, A.R.E., (1977), *The African buffalo: A study of resource limitation of populations,* University of Chicago Press, Chicago, p.511.

Skarpe *et al.*, (2004), *The return of the giants: Ecological effects of an increasing elephant population,* Ambio, 33(6): 276-282.

Slater, J. & Jones, R.J., (1971), *Estimation of the diets selected by grazing animals from microscopic analyses of feces – a warning,* Journal of the Australian Institute for Agricultural Science, 37: 238-240.

Solomon, E.P., Berg, L.R., & Martin, D.W., (1999), *Biology,* 5th Edition, Cengage Learning, Florence, Kentucky.

Spinage, C.A., (1986), *The natural history of antelopes,* Croom Helm, Beckenham.

SPSS Incorporated, 233 S. Wacker Drive, Chicago, Illinois, U.S.A

StatSoft Incorporated, 2300 East 14th Street, Tulsa, Oklahoma, U.S.A.

Stephens, D.W. & Krebs, J.R., (1986), *Foraging theory,* Princeton, Princeton University Press.

Stewart, D.R.M, (1967), *Analyses of plant epidermis in faeces: a technique for studying the preferences of grazing herbivores,* Journal of Applied Ecology, 4: 83-111.

Stewart, D.R.M., & Stewart, J., (1970), *Food preference data by faecal analyses for African plains ungulates,* Zoologica Africana, 15(1): 115.

Stowe, T., (2003), *Nutrient content of floodplain grasses and ruminant feces in the Okavango Delta,* Biological and Biomedical Sciences, Hope College, UK.

Talbot, L.M. & Talbot, M.H., (1963), *The wildebeest in western Masailand, east Africa,* Wildlife Monograph no.12, The Wildlife Society, Washington DC.

Townsend, C.R., Begon, M. & Harper, J.L., (2000), *Essentials of Ecology,* 2nd Edition, Wiley-Blackwell Science, Oxford, England.

Treisman, M., (1975), *Predation and the evolution of gregariousness. I. Models for concealment and evasion,* Animal Behaviour, 23: 779-800.

Valeix, M., Fritz, H., Matsika, R., Matsvimbo, F. & Madzikanda, H., (2007), *The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores,* African Journal of Ecology, 46: 402-410.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W., (2009), *Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use,* Ecology, 90: 23-30.

Vanderwalle, M., (2000), *Feeding area selection by zebra and wildebeest in relation to grassland composition, phenology and height,* Chapter 3, Phd. Thesis, University of the Witwatersrand, Johannesburg, South Africa.

Varian Incorporated, 3120 Hansen Way, Palo Alto, California, USA.

Van Oudtshoorn, F., (1999), *Guide to grasses of southern Africa*, 2nd edition. Briza

Walker, B.H., (1976), *An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation,* South African Journal of Wildlife Research, 6(1): 1-32.

Walker, B.H., (1993), *Rangeland ecology: Understanding and managing change,* Ambio, 22(2/3): 80-87.

Walther, F.R., (1990), *Reedbucks, waterbucks, and impalas,* In: Grzimek's Encyclopedia of Mammals, (Ed. Parker, S. P.), New York: McGraw-Hill. Volume 5, p. 448-461.

Western, D., (1975), *Water availability and it's influence on the structure and dynamics of a savannah large mammal community,* East African Wildlife Journal, 13: 265-286.

Westoby, M., (1974), *An analysis of diet selection by large generalist herbivores,* American Naturalist, 108(961): 290.

Williamson, D.T., (1990), *Habitat selection by red lechwe,* African Journal of Ecology, 28(2): 89-101.

Wilson, J.R., (1981), *Environmental and nutritional factors affecting herbage quality,* In: Hacker, J.B. (ed.), Nutritional limits to animal production from pastures, p.111-129, Proceedings of an international congress, St. Lucia, Queensland, CAB International.

Wilson, D.E. & Reeder, D.A.M., (1993), *Mammal species of the world,* Smithsonian Institution Press, Washington DC.

Winkler, A., (1992), *The feeding ecology of the Cape mountain zebra in the Mountain Zebra National Park, South Africa,* MSc. Thesis, University of the Witwatersrand, Johannesburg, South Africa.

Wirsing, A.J., Heithaus, M.R. & Dill, L.M., (2007), *Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators,* Animal Behavior 74:93-101.

Wrench, J.M., Meissner, H.H., & Grant, C.C., (1997), *Assessing diet quality of African ungulates from faecal analyses: the effect of forage quality, intake and herbivore species.* Koedoe, 40 (1):125-136.

APPENDIX 1

Table 1: Walker 8-point scale for determining the relative greenness of grass species.

Class	Relative Greenness	Mid-value
1	0%	0%
2	1-10%	5.5%
3	10-25%	17.5%
4	26-50%	38%
5	51-75%	63%
6	76-90%	83%
7	90-99%	94.5%
8	100%	100%

APPENDIX 2

Table 1: Arcsine transformed seasonal dietary proportions obtained for puku and lechwe through the methods of direct observation and faecal analyses.

		Seasonal prop.		Arcsine prop.		Std. err. arcsine prop.		Lower CI arcsine prop.		Upper CI arcsine prop.	
	Grass species	HWS	LWS	HWS	LWS	HWS	LWS	HWS	LWS	HWS	LWS
Puku	A. adscensionis		0.007		0.007				0.007		0.007
	A. macrum	**0.129**	0.083	0.164	0.122	0.011	0.009	0.142	0.105	0.186	0.139
	B. dura	0.019	0.041	0.020	0.046	0.010	0.004	0.001	0.038	0.040	0.054
	B. eruciformis	0.076	0.016	0.095	0.023	0.012	0.010	0.073	0.003	0.118	0.044
	B. humidicola	0.063	0.014	0.078	0.014	0.012	0.002	0.055	0.010	0.100	0.019
	B. nigropedata	0.022		0.028		0.014		0.001		0.054	
	C. dactylon	**0.258**	**0.256**	0.333	0.366	0.012	0.007	0.310	0.351	0.356	0.380
	C. gayana	0.020	0.002	0.022	0.002	0.007		0.008	0.002	0.036	0.002
	D. aegyptium	0.002	0.009	0.002	0.010			0.002	0.010	0.002	0.010
	D. eriantha	**0.110**	**0.122**	0.130	0.157	0.010	0.007	0.111	0.144	0.149	0.170
	E. colona	0.013		0.013		0.005		0.005		0.022	
	Eragrostis spp.	**0.112**	0.092	0.145	0.111	0.014	0.006	0.119	0.099	0.172	0.123
	P. deusteum		0.014		0.014		0.003		0.008		0.021
	P. mauritianus	0.077	0.084	0.103	0.119	0.013	0.008	0.077	0.104	0.129	0.135
	P. repens	0.020		0.027				0.027		0.027	
	P. scrobiculatum	0.009	0.047	0.009	0.063		0.007	0.009	0.050	0.009	0.076
	S. pyramidalis		0.001		0.001				0.001		0.001
	S. sphacalata	0.009	0.001	0.009	0.001	0.002		0.004	0.001	0.014	0.001
	T. spicatus		0.002		0.002		0.001		0.0004		0.003
	V. cuspidata		0.047		0.062		0.008		0.047		0.078
	V. nigritana	0.062	**0.164**	0.081	0.232	0.013	0.008	0.055	0.216	0.107	0.248

Table 1 continued…

Puku faecal	A. adscensionis	0.020	0.018	0.020	0.018		0.001	0.020	0.017	0.020	0.019
	A. macrum	**0.127**	**0.110**	0.127	0.111	0.010	0.001	0.107	0.108	0.147	0.113
	B. dura	0.007	0.089	0.007	0.089		0.001	0.007	0.087	0.007	0.090
	B. eruciformis	**0.220**	0.063	0.228	0.064	0.033	0.003	0.163	0.058	0.292	0.070
	B. humidicola	0.013	0.064	0.013	0.064		0.001	0.013	0.062	0.013	0.067
	B. nigropedata	0.063	0.012	0.063	0.012	0.007	0.001	0.050	0.011	0.077	0.014
	C. dactylon	**0.193**	**0.215**	0.195	0.218	0.017	0.003	0.162	0.212	0.229	0.224
	C. gayana		0.013		0.013		0.000		0.012		0.014
	D. aegyptium		0.006		0.006		0.000		0.005		0.006
	D. eriantha	**0.190**	0.058	0.193	0.058	0.023	0.001	0.149	0.056	0.237	0.060
	E. colona	0.007	0.000	0.007				0.007		0.007	
	Eragrostis spp.	0.027	0.035	0.027	0.035		0.001	0.027	0.034	0.027	0.037
	P. deusteum		0.030		0.030		0.001		0.029		0.032
	P. mauritianus	0.040	0.093	0.040	0.094	0.007	0.001	0.027	0.091	0.053	0.096
	P. repens		0.028		0.028		0.001		0.026		0.029
	P. scrobiculatum	0.047	0.051	0.047	0.051	0.016	0.001	0.016	0.050	0.077	0.053
	T. spicatus		0.019		0.019		0.001		0.018		0.020
	T. triandra		0.001		0.001				0.001		0.001
	V. cuspidata		0.009		0.009		0.000		0.008		0.010
	V. nigritana	0.047	0.085	0.047	0.085	0.006	0.001	0.034	0.082	0.059	0.088
Lechwe	A. macrum	**0.210**	0.096	0.313	0.136	0.105	0.088	0.107	-0.037	0.520	0.309
	A. schirensis	0.008		0.008				0.008		0.008	
	A. stipitata		0.006		0.006				0.006		0.006
	B. dura	0.019	0.010	0.020	0.010	0.061		-0.099	0.010	0.139	0.010
	B. humidicola	0.015	0.004	0.016	0.004			0.016	0.004	0.016	0.004
	C. dactylon	**0.399**	**0.306**	0.558	0.447	0.065	0.078	0.430	0.293	0.685	0.600
	D. eriantha	0.028	**0.102**	0.028	0.128	0.027	0.070	-0.024	-0.010	0.080	0.265
	E. colona		0.013		0.014			0.000	0.014		0.014
	Eragrostis spp.	0.086	0.026	0.104	0.028	0.076	0.041	-0.045	-0.053	0.252	0.109
	P. deusteum	0.017	0.090	0.018	0.106	0.014	0.060	-0.011	-0.013	0.046	0.225
	P. mauritianus	**0.148**	**0.213**	0.220	0.301	0.079	0.075	0.066	0.154	0.374	0.449
	P. repens	0.021		0.026				0.026		0.026	
	P. scrobiculatum	0.007	0.082	0.007	0.103	0.003	0.063	0.001	-0.020	0.014	0.226
	S. sphacelata	0.013		0.013		0.002		0.010		0.016	
	T. spicatus		0.002		0.002				0.002		0.002
	V. cuspidata	0.015	0.023	0.016	0.025		0.050	0.016	-0.073	0.016	0.123
	V. nigritana	0.014	0.028	0.015	0.039	0.029	0.107	-0.042	-0.171	0.071	0.249

Table 1 continued…

Lechwe faecal	A. macrum	0.095	**0.134**	0.095	0.134	0.005	0.002	0.086	0.129	0.104	0.139
	A. schirensis		0.002		0.002				0.002		0.002
	B. dura	0.075	0.067	0.075	0.068	0.007	0.003	0.062	0.062	0.088	0.073
	B. humidicola	0.050	0.042	0.050	0.043	0.004	0.002	0.042	0.038	0.058	0.047
	C. dactylon	**0.223**	**0.199**	0.224	0.201	0.007	0.003	0.211	0.195	0.237	0.207
	D. eriantha	0.053	0.072	0.053	0.072	0.005	0.002	0.043	0.069	0.062	0.076
	E. colona		0.038		0.038		0.001		0.036		0.041
	Eragrostis spp.	0.033	0.040	0.033	0.040	0.010	0.002	0.013	0.037	0.053	0.043
	P. deusteum	0.005	0.046	0.005	0.046		0.001	0.005	0.044	0.005	0.047
	P. mauritianus	**0.188**	**0.170**	0.188	0.171	0.008	0.003	0.173	0.164	0.204	0.177
	P. repens	0.025		0.025				0.025		0.025	
	P. scrobiculatum	0.068	0.068	0.068	0.068	0.004	0.001	0.061	0.066	0.074	0.071
	S. sphacelata	0.040		0.040		0.004		0.031		0.049	
	T. triandra		0.005		0.005		0.001		0.003		0.007
	V. cuspidata	0.005	0.009	0.005	0.009		0.0003	0.005	0.008	0.005	0.009
	V. nigritana	**0.143**	**0.108**	0.143	0.108	0.008	0.002	0.128	0.105	0.158	0.112

APPENDIX 3

Table 1: Seasonal proportional habitat use of puku and lechwe compared between species and to availability.

Proportion	Puku		Lechwe		Available	
	LWS	HWS	LWS	HWS	LWS	HWS
Shallow swamp	0.021		0.128	0.273	0.086	0.199
Interface zone	0.103	0.124	0.314	0.182	0.038	0.093
Low lying floodplains	0.371	0.056	0.302	0.273	0.341	0.060
High lying floodplains	0.381	0.112	0.151	0.182	0.459	0.333
Grasslands	0.124	0.124	0.105	0.061	0.057	0.046
Shrublands		0.551				0.241
Woodlands		0.022				0.009
Termitaria		0.011		0.030	0.019	0.019
Ratio	Puku:Available		Lechwe:Available		Puku:Lechwe	
	LWS	HWS	LWS	HWS	LWS	HWS
Shallow swamp	0.238		1.479	1.370	0.161	
Interface zone	2.725	1.335	8.297	1.964	0.328	0.680
Low lying floodplains	1.090	0.933	0.888	4.531	1.228	0.206
High lying floodplains	0.830	0.337	0.329	0.545	2.523	0.618
Grasslands	2.180	2.670	1.844	1.309	1.182	2.039
Shrublands		2.287				
Woodlands		2.427				
Termitaria		0.607		1.636		0.371

Table 1 continued…

STD. error	Puku:Available		Lechwe:Available		Puku:Lechwe	
	LWS	HWS	LWS	HWS	LWS	HWS
Shallow swamp	0.720		0.328	0.315	0.754	
Interface zone	0.398	0.354	0.307	0.426	0.339	0.465
Low lying floodplains	0.151	0.511	0.179	0.391	0.210	0.519
High lying floodplains	0.141	0.313	0.262	0.382	0.286	0.474
Grasslands	0.343	0.418	0.380	0.752	0.415	0.741
Shrublands		0.154				
Woodlands		0.992				
Termitaria		1.111		1.102		1.399

Confidence Intervals	Puku:Available				Lechwe:Available				Puku:Lechwe			
	LWS		HWS		LWS		HWS		LWS		HWS	
	Lower CI	Upper CI	Lower CI	Upper CI	Lower CI	Upper CI	Lower CI	Upper CI	Lower CI	Upper CI	Lower CI	Upper CI
Shallow swamp	0.058	0.977			0.777	2.815	0.738	2.542	0.037	0.707		
Interface zone	1.249	5.944	0.667	2.669	4.548	15.139	0.852	4.528	0.169	0.638	0.273	1.690
Low lying floodplains	0.811	1.464	0.343	2.541	0.625	1.261	2.105	9.757	0.813	1.854	0.074	0.570
High lying floodplains	0.630	1.095	0.182	0.623	0.197	0.549	0.258	1.152	1.440	4.423	0.244	1.566
Grasslands	1.112	4.273	1.176	6.062	0.876	3.883	0.300	5.713	0.524	2.668	0.477	8.718
Shrublands			1.690	3.094								
Woodlands			0.347	16.963								
Termitaria			0.069	5.353			0.189	14.196			0.024	5.759

Table 2: Seasonal proportional vegetation class use of puku and lechwe compared between species and to availability.

Proportion	Puku		Lechwe		Available	
	LWS	HWS	LWS	HWS	LWS	HWS
Annual hydrophytic		0.011			0.043	0.047
Annual helophytic	0.041		0.140	0.030	0.035	0.009
Annual xerophytic	0.010		0.023		0.027	
Perennial xerophytic	0.072	0.034	0.023	0.030	0.084	0.066
Perennial helophytic	0.660	0.292	0.419	0.364	0.622	0.498
Combretum spp.		0.090				0.094
Perennial hydrophytic	0.144	0.067	0.326	0.515	0.092	0.061
Annual or perenial	0.072	0.034	0.070	0.061	0.097	0.080
Croton megaloboris		0.191				0.113
Capparis tomentosa		0.202				0.014
Erythroxylum zambesiacum		0.056				
Baikea plurijuga		0.022				0.019
Ratio	Puku:Available		Lechwe:Available		Puku:Lechwe	
	LWS	HWS	LWS	HWS	LWS	HWS
Annual hydrophytic		0.239				
Annual helophytic	1.174		3.971	3.227	0.296	
Annual xerophytic	0.381		0.860		0.443	
Perennial xerophytic	0.861	0.513	0.278	0.461	3.103	1.112
Perennial helophytic	1.061	0.587	0.673	0.731	1.576	0.803
Combretum spp.		0.957				
Perennial hydrophytic	1.571	1.105	3.543	8.441	0.443	0.131
Annual or perenial	0.742	0.422	0.717	0.759	1.034	0.556
Croton megaloboris		1.695				
Capparis tomentosa		14.360				
Erythroxylum zambesiacum						
Baikea plurijuga		1.197				

Table 2 continued…

STD. error	Puku:Available		Lechwe:Available		Puku:Lechwe	
	LWS	HWS	LWS	HWS	LWS	HWS
Annual hydrophytic		1.041				
Annual helophytic	0.560		0.382	1.210	0.558	
Annual xerophytic	1.043		0.765		1.216	
Perennial xerophytic	0.403	0.624	0.720	1.018	0.788	1.137
Perennial helophytic	0.083	0.179	0.133	0.240	0.147	0.283
Combretum spp.		0.399				
Perennial hydrophytic	0.296	0.477	0.225	0.317	0.292	0.429
Annual or perenial	0.397	0.613	0.424	0.724	0.536	0.890
Croton megaloboris		0.291				
Capparis tomentosa		0.611				
Erythroxylum zambesiacum						
Baikea plurijuga		0.857				

Confidence intervals	Puku:Available				Lechwe:Available				Puku:Lechwe			
	LWS		HWS		LWS		HWS		LWS		HWS	
	Lower CI	Upper CI	Lower CI	Upper CI	Lower CI	Upper CI	Lower CI	Upper CI	Lower CI	Upper CI	Lower CI	Upper CI
Annual hydrophytic			0.031	1.842								
Annual helophytic	0.391	3.519			1.878	8.397	0.301	34.604	0.099	0.882		
Annual xerophytic	0.049	2.944			0.192	3.856			0.041	4.804		
Perennial xerophytic	0.391	1.896	0.151	1.741	0.068	1.138	0.063	3.391	0.662	14.539	0.120	10.321
Perennial helophytic	0.901	1.250	0.413	0.833	0.518	0.875	0.456	1.170	1.183	2.100	0.461	1.400
Combretum spp.			0.438	2.092								
Perennial hydrophytic	0.879	2.808	0.434	2.814	2.278	5.511	4.531	15.724	0.250	0.786	0.056	0.303
Annual or perenial	0.341	1.615	0.127	1.405	0.312	1.647	0.184	3.137	0.362	2.959	0.097	3.182
Croton megaloboris			0.959	2.997								
Capparis tomentosa			4.338	47.532								
Erythroxylum zambesiacum												
Baikea plurijuga			0.223	6.416								